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Bulletin of the British Museum (Natural History)

A guide to the species of the genus *Aspidisca*

Irene C. H. Wu & Colin R. Curds

Zoology series Vol 36 No 1 28 June 1979

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A guide to the species of the genus *Aspidisca*

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Introduction

As a sequel to 'A guide to the species of the genus *Euplotes*' (Curds, 1975) the present paper is primarily a collection of diagrams and descriptions of the species of the genus *Aspidisca* Ehrenberg, 1830 (1832). Keys to what we consider to be distinct species are included, and are designed to enable workers to make specific identifications of *Aspidisca* without the need to search the literature. Previous attempts known to the present authors are those of Plough (1916) who devised a key to eight species (see Appendix 1) and Kahl (1932) whose key included 28 species (see Appendix 2). Borror (1972), in a revision of the order Hypotrichida Stein, 1859, listed 22 species of *Aspidisca* with their synonyms. While we sometimes do not agree with Borror (1972), it should be pointed out that some of the disagreements are only matters of opinion. Information is still required to substantiate these opinions even though some effort has recently (Tuffrau, 1964; Borror, 1972; Curds, 1975, 1977) been devoted to the taxonomy of the family Euplotidae Ehrenberg, 1838. Since Ehrenberg, 1830 (1832) established the genus *Aspidisca* with *Aspidisca lynceus* (Müller, 1773) Ehrenberg, 1830 as the type species, over 50 nominal species have been transferred and added to the genus. Species have been distinguished by the size and shape of the body, the number of dorsal ribs, the presence of a thorn on the dorsal surface, the number of cirri on the ventral surface, nuclear features and the configuration of the peristome. Kahl (1932) applied all these criteria in devising his key (Appendix 2) and divided them into marine and freshwater species. Plough (1916), on the other hand, considered the shape of the 'cuirass' to be the most stable character and believed that the numbers and disposition of cirri to be variable. More recently, silver-impregnation techniques have been used to study the morphology and morphogenesis of ciliates. The diagnostic value of the silver-line systems of *Aspidisca* spp. and the other features mentioned above will be discussed under separate headings.

Features of taxonomic importance

(a) Habitat

The freshwater species listed by Kahl (1932) include *A. lynceus*, *A. costata*, *A. turrita*, *A. herbicola*, *A. marsupialis* and *A. sulcata*. Earlier Plough (1916) had reported the occurrence of *A. turrita* and *A. costata* in both seawater and freshwater but stated the others, including *A. lynceus*, to be strictly marine species. In fact the original specimens of *A. lynceus* were found in freshwater and the species has since been reported in freshwater sites (Kahl, 1932; Bick, 1972). *A. herbicola* Kahl, 1932 appears to be the only species which is reported to occur in freshwater alone. All other species described to date inhabit the marine environment.

(b) Size

It is known that the size of a ciliate may vary with many factors including rate of growth, concentration of food, kind of food and so on, and is therefore of limited taxonomic value (see Curds, 1975). In the case of *Aspidisca*, while their sizes range from 16 to 150 μm long most species are between 50 and 100 μm long (Fig. 1). Therefore, the exceptionally large size (135–150 μm) of *A. magna* Kahl, 1932 can perhaps justifiably be regarded as diagnostic.

(c) Shape

The typical shape of *Aspidisca* is oval although it generally tends to be more convex on the right than on the left. The outline may be smooth or jagged with spurs or dentations which mostly appear on the left border. The dorsal surface is commonly arched and it may be smooth

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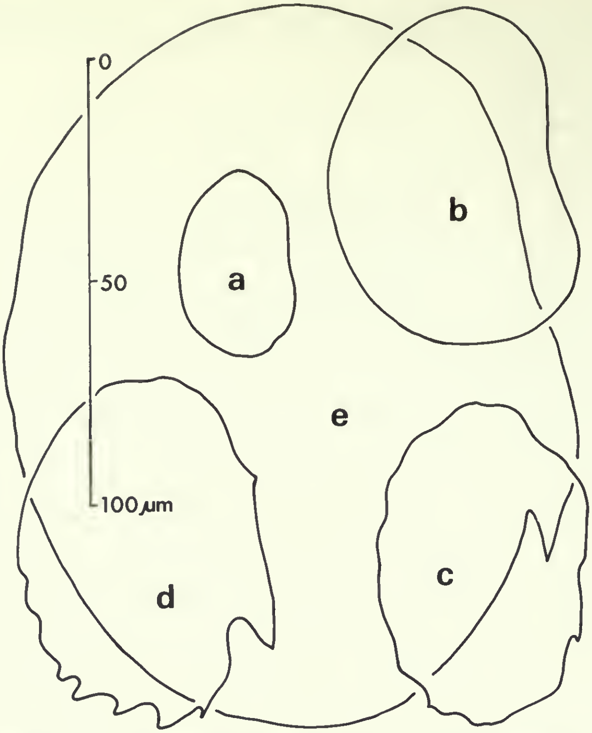

Fig. 1 Sizes of some *Aspidisca* species: (a) *A. polystyla*; (b) *A. magna*; (c) *A. lyncaster* (called *A. leptaspis* in this revision); (d) *A. pulcherrima*; (e) *A. magna* (after Tuffrau, 1964).

or longitudinally marked by indistinct furrows, conspicuous ribs and sometimes a posteriorly directed curving thorn.

Plough (1916) distinguished species primarily by the number of spurs on the left border and indeed, by the relatively crude earlier diagrams, the number of spurs does appear to be the most distinctive feature among the species Plough included (Fig. 2). More specimens with serrated borders have since been studied in greater detail. In many cases the actual number of spurs present and the degree to which they are developed is variable and there is considerable difference between descriptions (Fig. 3). However, a projection from the peristomial area on the left border is found on all species with serrated borders. Thus we do not intend to separate species by the number of peripheral serrations but consider the presence of a 'peristomial spur' diagnostic.

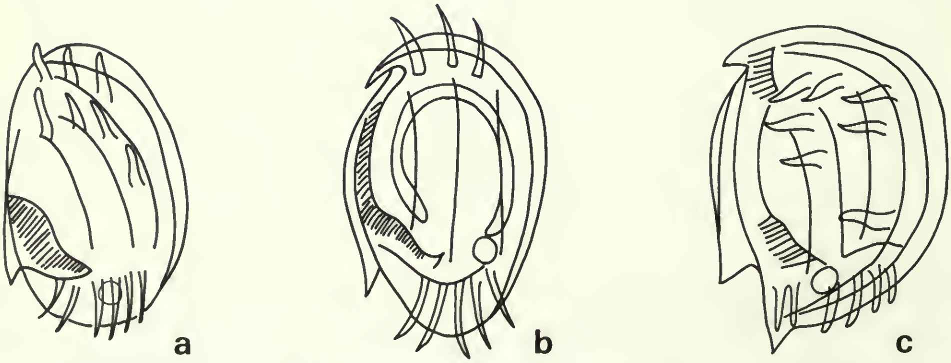

Fig. 2 Ventral surfaces of : (a) *Aspidisca hexeris* (called *A. sedigita* in this revision); (b) *A. lyncaster*; (c) *A. sedigita* (after Plough, 1916).

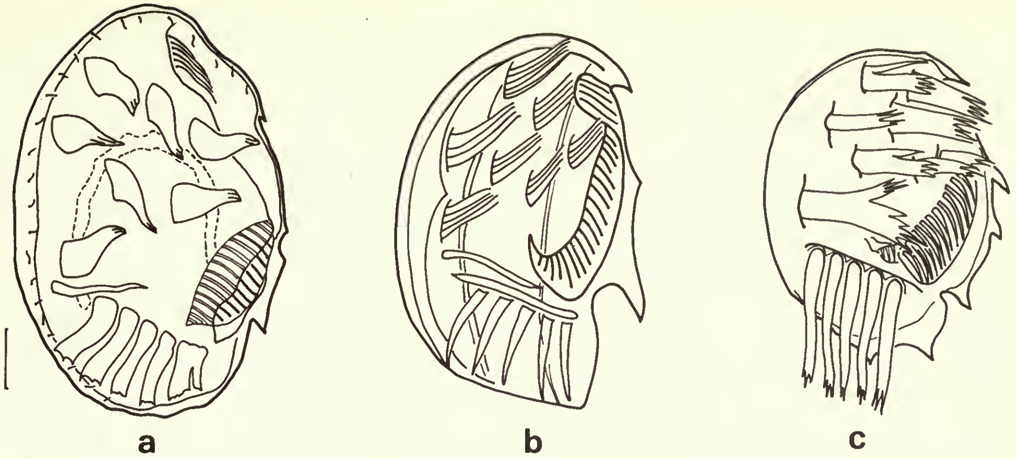

Fig. 3 Ventral surface of *Aspidisca lyncaster* (called *A. leptaspis* in this revision): (a) after Tuffrau, 1964; (b) after Kahl, 1932; (c) after Dragesco, 1960.

(d) Dorsal ribs and thorn

Many workers have reported that the dorsal ribs and thorn noted in several species of *Aspidisca* are inconsistent in size, number and even their presence. Diller (1975) stated that his specimens of *A. costata* usually had six to seven dorsal ribs but the number varied considerably within the three to ten range. Hamm (1964) showed that the size of the dorsal ribs of *A. costata* vary under different growth conditions (Fig. 4). The dorsal thorn of *A. turrita* has also been found to vary in size (Ehrenberg 1838; Claparède & Lachmann 1858). Kahl (1932) stated that this thorn is sometimes missing while Borror (1965) mentioned that a dorsal thorn was present on only some of his specimens of *A. aculeata* (Ehrenberg, 1838) Kahl, 1932. However, in both cases there are insufficient data to be certain that the specimens with and without a dorsal thorn are the same species. In the following keys, the actual presence of ribs, crenated ribs or thorn on the dorsal surface will be used as diagnostic characters but their number and size will be regarded as taxonomically insignificant. More conclusive studies of clonal cultures of *Aspidisca* with dorsal ribs, thorn and peripheral projections would be most valuable, particularly so as variable dorsal ridges and lateral projections have been recently noted (Curds, 1977) in a related hypotrich, *Euplotes aediculatus*.

(e) The adoral zone of membranelles

The genus *Aspidisca* is characterised by a two-part adoral zone of membranelles (AZM) along the left border. The posterior part is a series of 8–20 membranelles lining the peristome which is partially enclosed by the ventral plate and the anterior part is a group of cilia-like structures, two to eight in number, often confined in an indentation of the ventral plate. Kahl (1932) and Dragesco (1965) regarded the configuration of the flap of ventral plate over the buccal cavity as

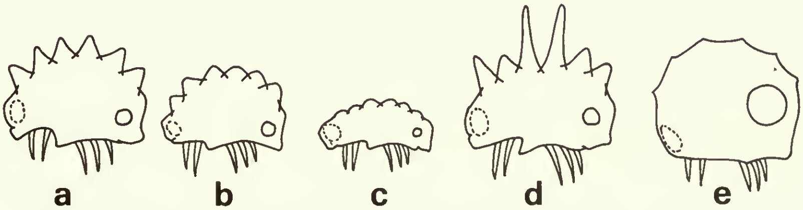

Fig. 4 *Aspidisca costata* showing dorsal ribs of: (a) normal type; (b) overfed form; (c) starved specimen; (d) specimen with extremely high ribs; (e) specimen from an adverse environment (called *A. cicada* in this revision after Hamm, 1964).

a specific character but we find it not sufficiently distinctive to be of significant taxonomic value. The peristome is generally triangular, about one third to half of the body size in length and one fourth to one third in width. In some cases, the peristome extends forward and almost meets the anterior group of ciliary structures which is referred to by different names in the literature and is often regarded as a specialised section of the AZM. We refer to this group of 'cilia' as the anterior ciliary organelle. Diller (1975), who called the organelle a 'tooth', stated that the differentiation of this and the AZM are independent in *A. costata* and suggested that it is equivalent to the I/1 cirrus in *Euplotes* (using the system of Wallengren 1900); this suggestion does not conform with the scheme for *Aspidisca* presented by Tuffrau (1964) (see Fig. 11). The numbers of membranelles in the posterior AZM and of the 'cilia' in the anterior ciliary organelle will be mentioned, if known, in the following descriptions even though they seem to have little diagnostic value.

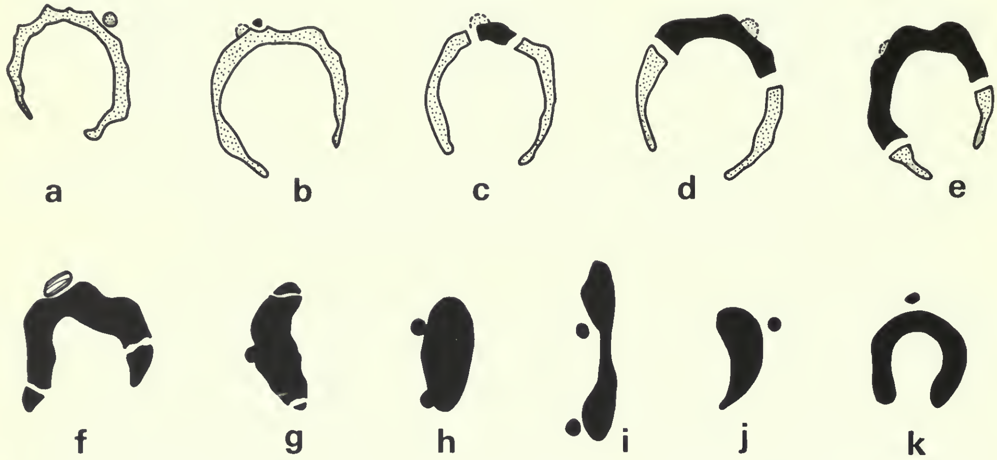

Fig. 5 Some stages of nuclear reorganisation in *Aspidisca lynceus*: (a) the macronucleus of a normal resting individual; (b) an early stage in the formation of the reorganisation band; (c) reorganisation bands completely separated by the central chromatin; (d) nucleus about one-half reorganised; (e) reorganisation about two-thirds complete; (f) the beginning of condensation. Micronucleus in prophase; (g) bands about to disappear; (h) macronucleus fully condensed; (i) constriction of the macronucleus; (j) daughter macronucleus slightly after division; (k) macronucleus of a young daughter individual (after Summers, 1935).

(f) Nuclear features

It has long been recognised that the nuclei of ciliates are of taxonomic importance. The macronucleus of hypotrichs such as *Euplotes* takes a variety of forms during reorganisation; however, during 'interphase' it is constant and characteristic of the species (see Curds, 1975). Most *Aspidisca* spp. have, like *Euplotes*, a C-shaped or horseshoe-shaped macronucleus and a spherical micronucleus and Summers (1935) described the division and reorganisation of the macronucleus of *A. lynceus* to be comparable to that of *Euplotes*. A band-like macronucleus has been described by Ghosh (1921) and several authors have illustrated horseshoe-shaped macronuclei with dilated centres. These may correspond to two of the divisional stages of the macronucleus of *A. lynceus* as illustrated by Summers (Fig. 5). A small number of species have been found to have two oval or ellipsoid macronuclei. While Tuffrau (1964) suggested that the presence of two macronuclei in *A. major* (Madsen, 1931) Kahl, 1932 might represent a transitional stage, this has not been confirmed and the presence of two macronuclei is used as a diagnostic character in the following keys. Summers (1935) stated that one micronucleus was present in trophic *A. lynceus*, but Borror (1965) found there were one to three micronuclei in his

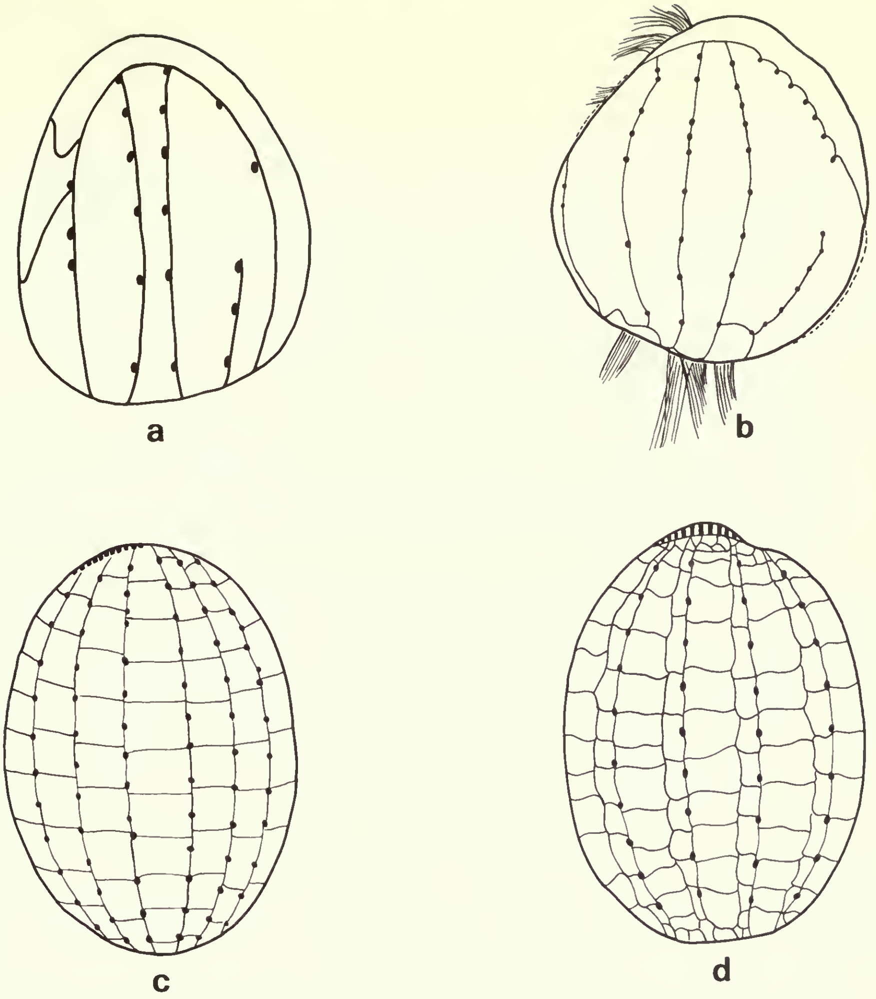

Fig. 6 Dorsal silver-line systems of: (a) *Aspidisca cicada* (after Curds, 1977); (b) *Aspidisca lynceus* (after Klein, 1929); (c) *Euplotes* sp., single-vannus type after Curds, 1975; (d) *Euplotes* sp., double-patella type after Curds, 1975.

specimens of *A. aculeata*. Agamaliev (1967, 1971) observed similar variation in *A. caspica* Agamaliev, 1967 while Dragesco (1954) described *A. hyalina* as possessing four micronuclei. Summers (1935) noted that although the division of the micronucleus is usually initiated when the reorganisation process of the macronucleus is about two thirds complete, it may be much earlier. Dini & Bracchi (1976) who studied the nuclear cycle of *A. aculeata* also found that division of the micronucleus preceded that of the macronucleus. Therefore the presence of two micronuclei may be a transitional state. On the other hand, Dini & Bracchi stated that 'when more micronuclei are present in the same cell, they divide asynchronously'. These data suggest that the number of micronuclei should not be used as a taxonomic criterion until the micronuclear activities of *Aspidisca* are better understood.

(g) Dorsal argyrome

It was hoped that the patterns of the dorsal argyrome or silver-line system of *Aspidisca* would be valuable for specific identification. Unfortunately, only a few workers have described the dorsal silver-line system of the species studied and some have encountered technical difficulties in applying the silver-impregnation methods to this genus although the ventral argyrome and

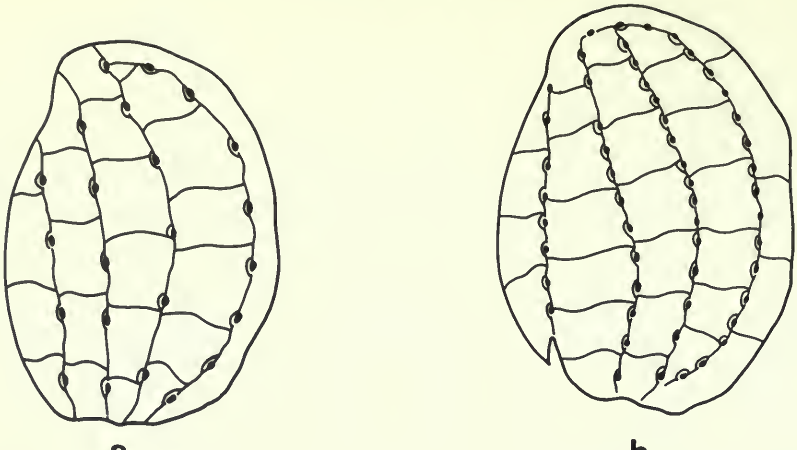

Fig. 7 Dorsal silver-line system of: (a) *Aspidisca aculeata*; (b) *Aspidisca leptaspis* (after Agamaliev, 1974).

cirral bases are usually successfully stained. Even Tuffrau (1964), who pioneered the application of the argyrome patterns for the diagnosis of *Euplotes*, only gave incomplete descriptions of the silver-line systems of *Aspidisca* spp. which he studied. Klein (1929) and Curds (1977) used the dry silver method (see Klein, 1958) to stain *A. lynceus* and *A. cicada* respectively. They found that both of these species have distinctly different argyrome patterns from those described in the genus *Euplotes* (Fig. 6). In neither case did the staining depict any connections between the kineties. However, *A. aculeata* and *A. leptaspis* Fresenius, 1865 have dorsal argyromes similar to those of *Euplotes* with four dorsal kineties connected by single links (Fig. 7). Furthermore, the silver-line systems of *A. polystyla* Stein, 1859 and *A. major* (Madsen, 1931) Kahl, 1932 were described by Tuffrau (1964) as having four kineties with argyrome patterns like those of *Euplotes eurystomus*. Agamaliev (1967, 1971) studied the silver-line system of *A. caspica* and found the dorsal argyrome pattern to be highly variable. He observed single, double and multiple rows of polygons between the kineties in this species and that the number of dorsal cilia was also highly variable (Fig. 8). Recently Gates & Curds (1979) noted that the geometry of the dorsal argyrome in different stocks of the same clone of *Euplotes* varies significantly. Because of the paucity of

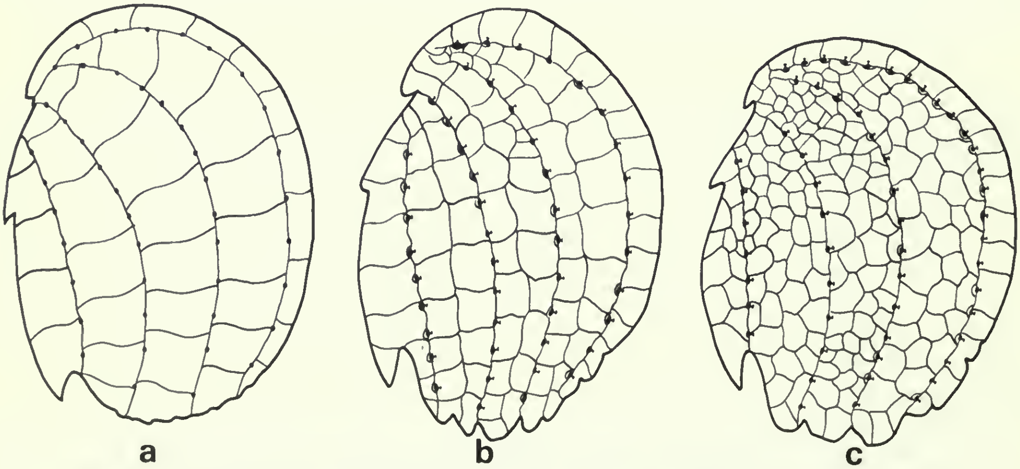

Fig. 8 Dorsal silver-line patterns of *Aspidisca caspica*: (a) after Agamaliev, 1967; (b & c) after Agamaliev, 1971.

data concerning the dorsal argyrome and its reported variability, we have not used it for specific identification but do add information on it when available.

(h) The cirri

We believe that the numbers and arrangements of the cirri on the ventral surface of *Aspidisca* are the most stable diagnostic features. With few exceptions, *Aspidisca* spp. have seven frontoventral and five transverse cirri. Some species have an extra satellite-like frontoventral cirrus making eight in total. Only *A. mutans* Kahl, 1932 and *A. binucleata* Kahl, 1932 have more than eight frontoventral cirri. The extreme left hand cirrus of the five transverse cirri is frequently split, often into three, making seven in all. One species, *A. polystyla*, is consistently found with 11–15 transverse cirri which the present authors regard as a reasonable specific character although it has been suggested (Tuffrau, 1964) that it is the result of three of the original transverse cirri splitting.

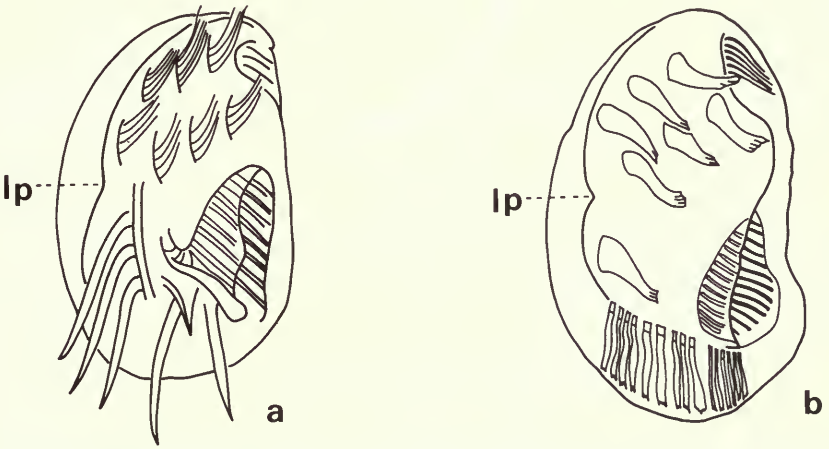

Fig. 9 Cirri arrangement: (a) *Aspidisca lynceus* showing 'lynceus-arrangement' of the frontoventral cirri (after Kahl, 1932); (b) *Aspidisca polystyla* showing 'polystyla-arrangement' of the frontoventral cirri (after Tuffrau, 1964).

The frontoventral cirri appear to be arranged in two basic patterns. One is as in *A. lynceus* where the seven frontoventral cirri are located within the anterior half of the ventral surface, with a row of four cirri running closely along the anterior right border and a row of three nearer the centre (Fig. 9a). The second is as in *A. polystyla* which was the first species to be described with six of the seven frontoventral cirri in the anterior half of the ventral surface, in two groups of three, and the remaining cirrus lying subequatorially in the posterior half of the body close to the transverse cirri (Fig. 9b). These cirri have frequently been referred to as six frontals and one ventral. There is often a low projection ('lp' in Fig. 9) on the inner right border dividing the ventral surface. These two patterns will be referred to as the 'lynceus-arrangement' and the 'polystyla-arrangement'. Where eight frontoventral cirri are observed, one cirrus is invariably satellite-like which does not affect the overall 'polystyla-arrangement' of the other seven cirri. Satellite-like cirri have been shown by Tuffrau (1964) and Deroux & Tuffrau (1965) to have distinct morphogenetic origins. These authors studied the morphogenesis of the cirri of *A. lyncaster* and *A. orthopogon* respectively and numbered the cirri as did Wallengren (1900) for *Euplotes* (Fig. 10a & b). Their system is adopted throughout this revision. Although it is erroneous to regard such cirri as true 'satellites', which many workers have done, the term 'satellite-like', while perhaps misleading, is probably most appropriate. A different morphogenetic pattern for the cirri and the AZM of *A. costata* was presented by Diller (1975) (Fig. 10c).

The location of the transverse cirri is fairly uniform throughout the genus. They are generally just posterior to the peristome in a row curving towards the anterior on the right. In some species, the three transverse cirri on the right form an almost vertical row slightly apart from the other two cirri. It may be significant that the latter arrangement of the transverse cirri appears to associate with frontoventral cirri in 'lynceus-arrangement' (see Fig. 11).

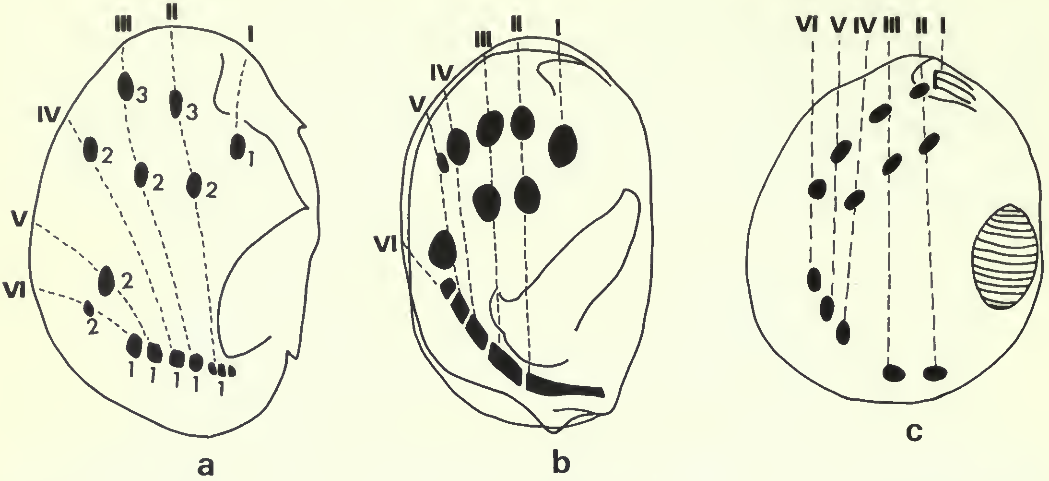

Fig. 10 Numeration of ventral cirri by the Wallengren (1900) system of: (a) *Aspidisca lyncaster* after Tuffrau, 1964 (called *A. leptaspis* in this revision); (b) *A. orthopogon* after Deroux & Tuffrau, 1965; (c) *A. lynceus* after Diller, 1975.

Diagnosis of *Aspidisca*

Small (mostly 50–100 μm) hypotrichs. Body ovoid and rigid. Dorsal and right side convex. Ventral surface flattened. Dorsal surface may be smooth or conspicuously ridged. Left and posterior borders sometimes serrated. AZM in two parts. The posterior part is a system of membranelles lining the peristome while the anterior part (or anterior ciliary organelle) is comprised of two to eight cilia. Seven to eight frontoventral cirri, five to twelve transverse cirri. No marginal or caudal cirri. Macronucleus horseshoe-shaped or in two rounded parts. Mostly marine, few euryhaline.

Systematic description

Keys to the genus *Aspidisca*

The characters selected to separate the species are used in order of their reported stability. The first division of species into groups is based on the number and arrangement of the frontoventral cirri. Further separations are based on the number of transverse cirri, presence of peristomial spur, presence of dorsal ribs and thorn, number of macronuclei and so on. Unless otherwise stated, all species described are marine, the sizes of organisms given in the text refer to their lengths and scales drawn on diagrams indicate 10 μm.

Key to the major groups

1 a	7 or 8 frontoventral cirri	2
b	more than 8 frontoventral cirri	**SECTION C** p. 27
2 a	frontoventral cirri in 'lynceus-arrangement'	**SECTION A** p. 9
b	frontoventral cirri in 'polystyla-arrangement'	**SECTION B** p. 14

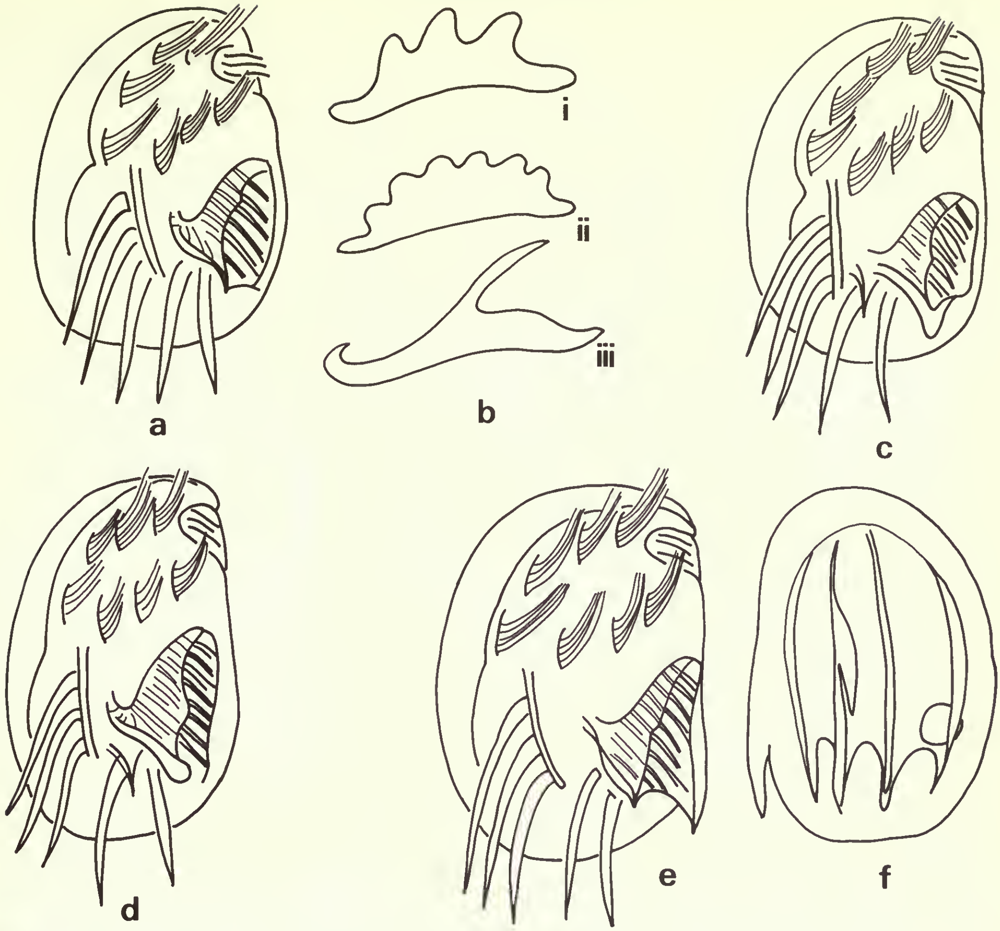

Fig. 11 Four *Aspidisca* species with lynceus-type ventral cirri arrangement (after Kahl, 1932): (a) *A. cicada* (called *A. costata* & *A. sulcata* in Kahl); (b) cross-section of (i) *A. cicada* (called *A. sulcata* in Kahl); (ii) *A. cicada* (called *A. costata* in Kahl), (iii) longitudinal section of *A. turrita*; (c) *A. turrita*; (d) *A. lynceus*; (e) *A. herbicola*, ventral surface; (f) *A. herbicola*, dorsal surface.

Section A

Key to species with frontoventral cirri in 'lynceus-arrangement'

1 a	with peristomial spur	6
b	without peristomial spur	2
2 a	dorsal surface smooth	*A. lynceus*
b	dorsal surface with grooves, ribs and/or thorn	3
3 a	with dorsal thorn	*A. turrita*
b	without dorsal thorn	4
4 a	3–10 conspicuous dorsal ribs	*A. cicada*
b	indistinct dorsal grooves	5
5 a	6 dorsal kineties bearing, from left to right 2 : 7 : 9 : 9 : 7 : 7 cilia	*A. lynceus*
b	5 dorsal kineties bearing, from left to right 3 : 6 : 6 : 3 : 2 cilia	*A. cicada*
6 a	with dorsal thorn	*A. herbicola*
b	without dorsal thorn	*A. lyncaster*

Aspidisca lynceus (Müller, 1773) Ehrenberg, 1830

Trichoda lynceus Müller, 1773
Aspidisca nana Tucolesco, 1962

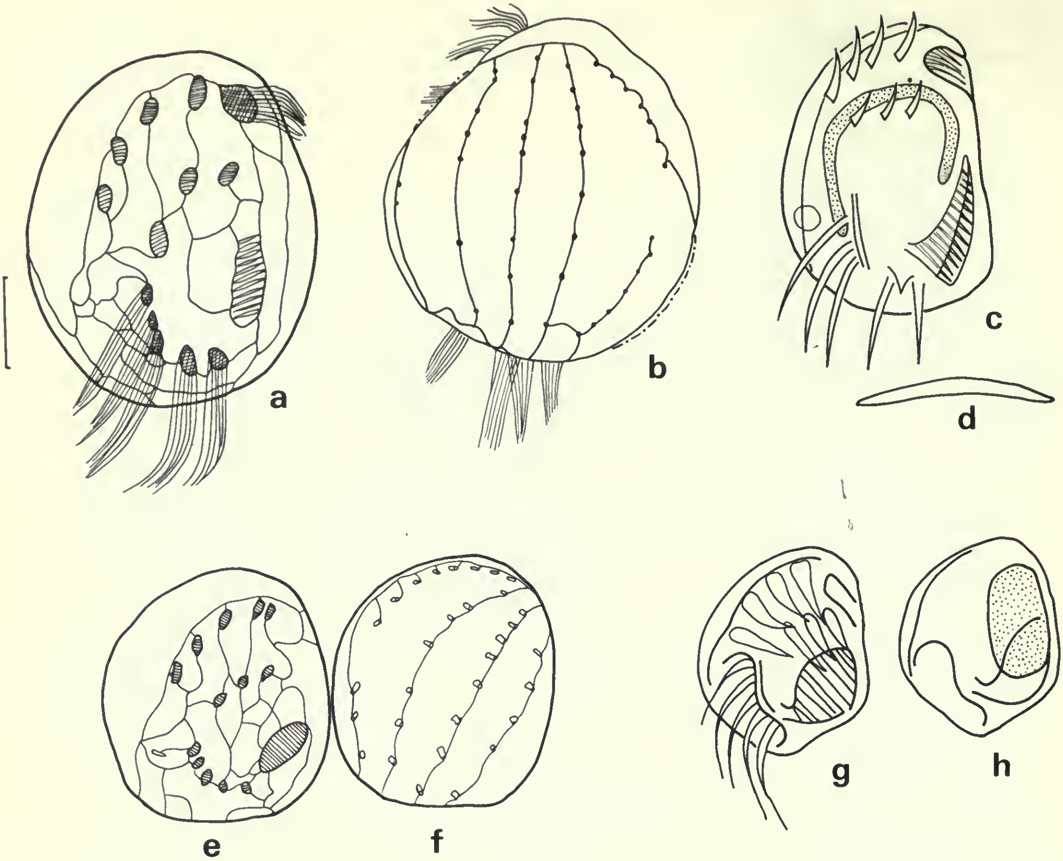

Fig. 12 . *Aspidisca lynceus*: (a & b) ventral & dorsal silver-line systems after Klein, 1929; (c & d) ventral surface & diagrammatic cross-section after Bick, 1972; (e & f) ventral & dorsal silver-line systems after Gelei, 1939; (g & h) ventral view & nucleus (called *A. nana* in Tucolesco, 1962).

This species was first described by Müller (1773) as *Trichoda lynceus* and was transferred to the genus *Aspidisca* by Ehrenberg (1830) as the type species. It is probably the most studied and widespread species of the genus and its general morphology has been described in detail by Claparède & Lachmann (1858), Stein (1859), Kahl (1932), Gelei (1939) and Bick (1972). Klein (1929) was the first to describe the silver-line system stained by the dry-silver method. Gelei (1939) also used the silver-impregnation technique but illustrated a silver-line system different to that shown by Klein. The original specimens were described from freshwater but others have been found in marine and freshwater habitats from various parts of the world.

Diagnosis. *Aspidisca lynceus* (Figs 11d & 12) is a small (30–50 μm) species found in all types of water where decomposition of organic material takes place, frequently in activated sludge. The typical features are oval body with straight left border and convex right border, smooth outline, seven frontoventral cirri, five transverse cirri, 10–15 membranelles in the posterior AZM and three to four cilia in the anterior ciliary organelle, a horseshoe-shaped macronucleus and a spherical micronucelus. The arrangement of the cirri is typical of a group of four species, *A. cicada*, *A. herbicola*, *A. lynceus* and *A. turrita* (Fig. 11). The frontoventral cirri are in two rows, of four and three cirri, near the anterior border; two of the five transverse cirri are immediately posterior to the peristome while the other three are slightly apart on the right and are almost vertically aligned. Kahl (1932) and Bick (1972) have noted a distinct spike-like projection separating the extreme left pair of transverse cirri in *A. lynceus* and this is also found in *A. turrita* (Figs 11c

& d, 12c). A smooth dorsal surface distinguishes *A. lynceus* from *A. cicada* which has dorsal ribs, but Stein (1859) noted three feeble dorsal furrows on his specimens of *A. lynceus*, while Hamm (1964) noted that the ribs of *A. cicada* are sometimes indistinct in which cases the separation of *A. lynceus* from *A. cicada* relied upon the dorsal silver-line system. The silver-line system of *A. lynceus*, according to Klein (1929), consists of two lateral peripheral kineties which meet anteriorly encircling three central longitudinal kineties and a short kinety on their right which extends only to the posterior half of the body. The kineties carry, from left to right, 2 : 7 : 9 : 9 : 7 : 7 cilia (Fig. 12b).

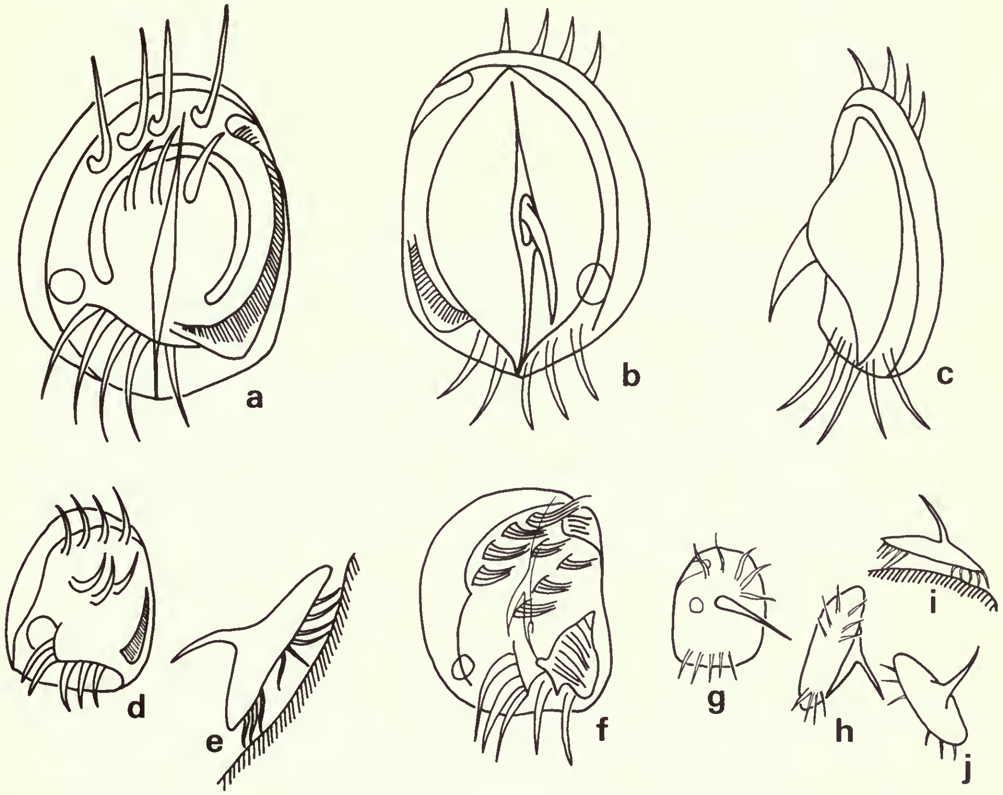

Fig. 13 *Aspidisca turrita*: (a–c) ventral, dorsal & dorsolateral view after Stein, 1859; (d & e) ventral & lateral view after Claparède & Lachmann, 1858; (f) after Kahl, 1932; (g–j) dorsal thorns (called *Euplotes turritus* in Ehrenberg, 1838).

Aspidisca turrita (Ehrenberg, 1838) Claparède & Lachmann, 1858

Euplotes turritus Ehrenberg, 1838

Ehrenberg (1838) first discovered this species, which is characterised by the presence of a dorsal thorn, among seaweeds in Berlin and later in freshwater together with *A. lynceus*. He named this organism *Euplotes turritus* but Claparède & Lachmann (1858) transferred it to the genus *Aspidisca* and emended the specific name to *turrita*. The latter authors noted that the dorsal thorn on their specimens found near Berlin was more prominent than that reported by Ehrenberg. The species was redescribed by Stein (1859), Plough (1916) and Kahl (1928, 1932). Kahl (1932) noted that its shape and ciliature are completely identical to those of *A. lynceus* and that there may be ribs as well as a thorn on the dorsal surface which itself may vary in size or be missing. Further studies may prove the dorsal thorn to be a transitional appendage, in which case *A. turrita* should be regarded as a synonym of *A. lynceus*.

DIAGNOSIS. *Aspidisca turrita* (Figs 11c & 13) is a euryhaline species and its morphology is almost identical to the type species *A. lynceus.* It is small (20–30 µm), the body is oval but convex on the right and the outline is smooth. There are seven frontoventral cirri in 'lynceus-arrangement' and, as in *A. lynceus*, two of the five transverse cirri are found posterior of the peristome separated by a 'spike'. The other three transverse cirri are aligned almost vertically near the right border. The macronucleus is C-shaped. A curved, pointed dorsal thorn distinguishes this from the type species.

Aspidisca cicada (Müller, 1786) Claparède & Lachmann, 1858

Trichoda cicada Müller, 1786
Coccudina cicada Bory, 1827
Coccudina crassa Dujardin, 1841
Aspidisca costata (Dujardin, 1841) Stein, 1859
Aspidiscopsis bengalensis Ghosh, 1921
Aspidisca marsupialis Penard, 1921
Aspidisca sulcata Kahl, 1932
Aspidisca costata f. *tetracirrata* Tucolesco, 1962

The taxonomic history of this species is one of confusion and misidentifications. Brown (1966) studied the species and subsequently (Brown, 1968) gave a complete historical account of the nomenclature of the species but the confusion remained. A recent account and redescription of the species was given by Curds (1977).

Briefly, the original freshwater specimens were described by Müller (1786) and named *Trichoda cicada* which Bory (1827) then transferred to the genus *Coccudina.* Claparède & Lachmann (1858) placed *T. cicada* Müller in the genus *Aspidisca.* Stein (1859) first synonymised *Coccudina costata* Dujardin, 1841 with *Aspidisca cicada* Claparède & Lachmann, 1858. However, the dorsal ribs of the former species were described as being crenated while those of the latter species were said to be smooth. Later workers including Plough (1916), Kahl (1932), Hamm (1964), Bick (1972) and Diller (1975) perpetuated the error and described *A. cicada* (Müller, 1786) Claparède & Lachmann, 1858 under the name *A. costata* (Dujardin, 1841) Stein, 1859. Borror (1972) also listed *A. cicada* as a synonym of *A. costata* and *Trichoda cicada* as a synonym of *A. lynceus.*

DIAGNOSIS. *Aspidisca cicada* (Fig. 14) is a small (20–45 µm) euryhaline species similar to the type species *A. lynceus* and equally widely distributed. The oval body is convex on the right and there are seven frontoventral and five transverse cirri. The frontoventral cirri are in 'lynceus-arrangement' and a projection separating the second and third transverse cirri from the left has been noted by Bick (1972) and Curds (1977). The body outline is smooth but the peristome sometimes form a 'swelling' at the posterior left. There are about eight membranelles in the posterior AZM and three anterior cilia. The dorsal surface is conspicuously ridged by longitudinal ribs varying in size and number (within the three to ten range). The macronucleus is C-shaped and the micronucleus is at its anterior left. The dorsal silver-line system consists of two central longitudinal kineties and on their right a short kinety extending only to the posterior third of the body, encircling these are two outer kineties which runs along the periphery and meet anteriorly. The five kineties, from left to right, carry 3 : 6 : 6 : 3 : 2 cilia.

Aspidisca herbicola Kahl, 1932

This species has been described once briefly and it is the only species that has not yet been found in marine habitats.

DIAGNOSIS. *Aspidisca herbicola* (Fig. 11e & f) is a small (50 µm) freshwater species. The peristomial spur and the four dorsal ribs, one bearing a thorn, distinguish this from the type species. The seven frontoventral cirri are in 'lynceus-arrangement'. The transverse cirri are arranged exactly like those of *A. lynceus* except that the two cirri on the left are not separated by a 'spike'. There are about ten membranelles in the posterior AZM and three anterior cilia.

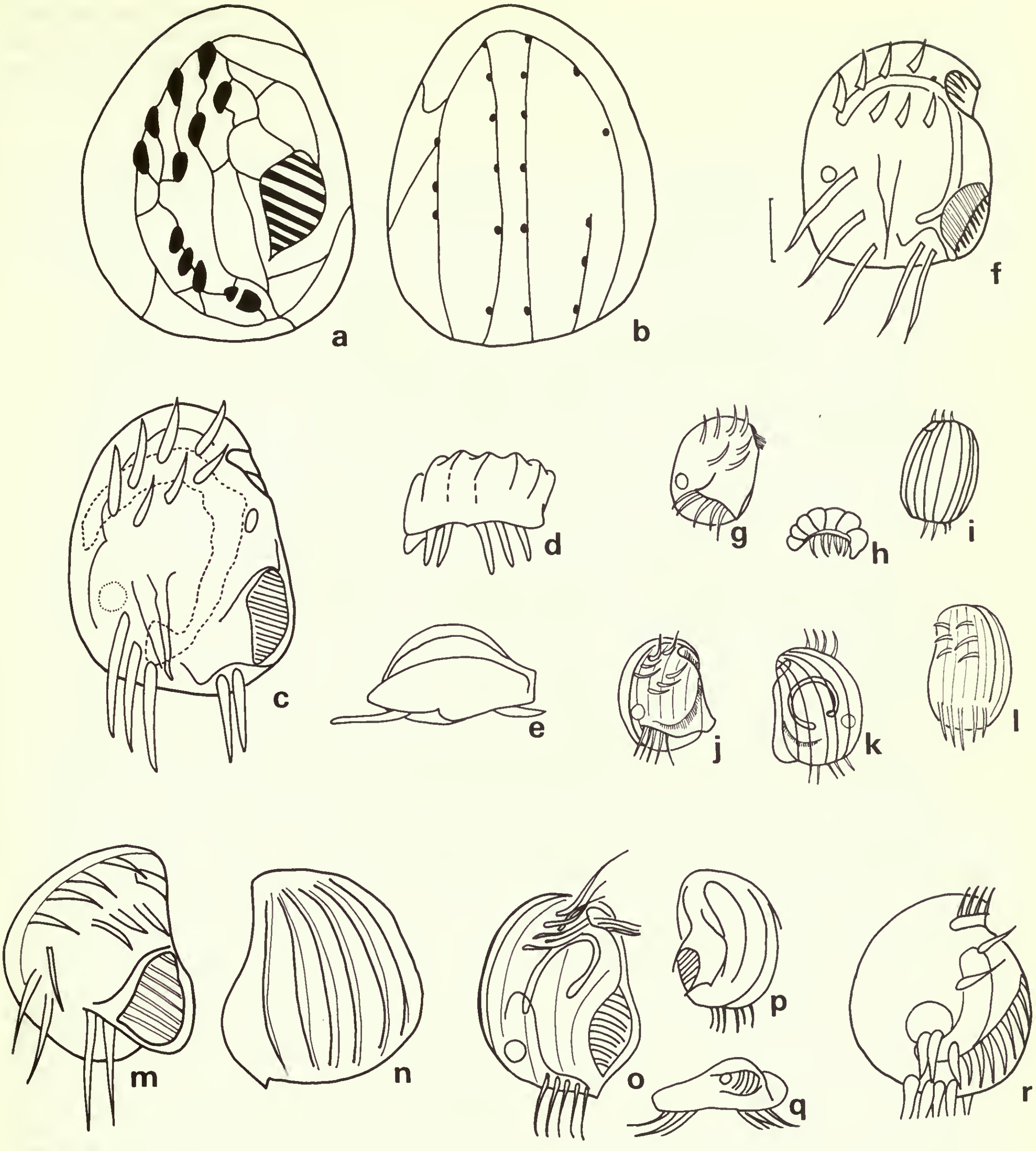

Fig. 14 *Aspidisca cicada*: (a–e) after Curds, 1977; (f) after Bick, 1972 (called *A. costata*); (g–i) after Claparède & Lachmann, 1858; (j–k) after Stein, 1859 (called *A. costata*); (l) after Dujardin, 1841 (called *Coccudina crassa*); (m–n) after Tucolesco, 1962 (called *A. costata* f. *tetracirrata*); (o–q) after Penard, 1921 (called *A. marsupialis*); (r) after Ghosh, 1921 (called *Aspidiscopsis bengalensis*).

Aspidisca lyncaster (Müller, 1779) Stein, 1859

Trichoda lyncaster Müller, 1779
Kerona lyncaster Müller, 1786

This species was first briefly described as *Trichoda lyncaster* by Müller in 1779 and later (1786) he transferred it to the genus *Kerona*. Stein (1859), by fixing the animals, gave a more detailed description of the specimens collected from seawater of Stralsundt, and later from Travemünde. The species was transferred to the genus *Aspidisca* by Stein in 1859. Plough (1916) redescribed the species in his work but later workers, including Kahl (1932), Dragesco (1960) and Tuffrau (1964), described organisms under the name *A. lyncaster*, which the present authors would regard as *A. leptaspis*.

DIAGNOSIS. *Aspidisca lyncaster* (Fig. 15) is a small (30–50 µm) species. It is almost egg-shaped, slightly pointed posteriorly. On the left border there is a conspicuous peristomial spur and a smaller anterior projection. There are seven frontoventral cirri in 'lynceus-arrangement' which distinguishes this species from *A. leptaspis*, five transverse cirri, an extensive peristome and two to three cilia in the anterior ciliary organelle. The dorsal surface is marked by three longitudinal ridges and the macronucleus is horseshoe-shaped.

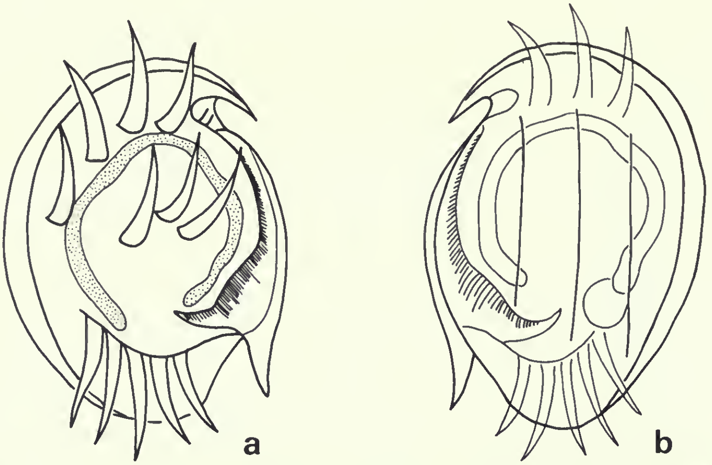

Fig. 15 *Aspidisca lyncaster*: (a) ventral surface; (b) dorsal surface (after Stein, 1859).

Section B

Key to species with frontoventral cirri in 'polystyla-arrangement'

1 a	7 frontoventral cirri	2
b	8 frontoventral cirri	11
2 a	5–7 transverse cirri	3
b	10–15 transverse cirri	***A. polystyla***
3 a	with peristomial spur	8
b	without peristomial spur	4
4 a	dorsal surface smooth.	5
b	dorsal surface with ridges, ribs and/or thorn	6
5 a	2 macronuclei	***A. major***
b	single macronucleus	***A. steini***
6 a	dorsal surface with ribs but without thorn	7
b	dorsal surface with ribs and a thorn	***A. aculeata***
7 a	dorsal ribs crenated	***A. tuberosa***
b	dorsal ribs not crenated	***A. polypoda***
8 a	dorsal surface with ribs and a thorn	***A. dentata***
b	dorsal surface without thorn	9
9 a	120–150 µm	***A. magna***
b	50–100 µm	10

10 a	2 macronuclei	***A. fusca***
b	single macronucleus	***A. sedigita***
11 a	without peristomial spur (with V/3 cirrus)	***A. orthopogon***
b	with peristomial spur (with VI/2 cirrus)	12
12 a	dorsal surface with smooth ridges	***A. leptaspis***
b	dorsal surface with crenated ribs	***A. pulcherrima***

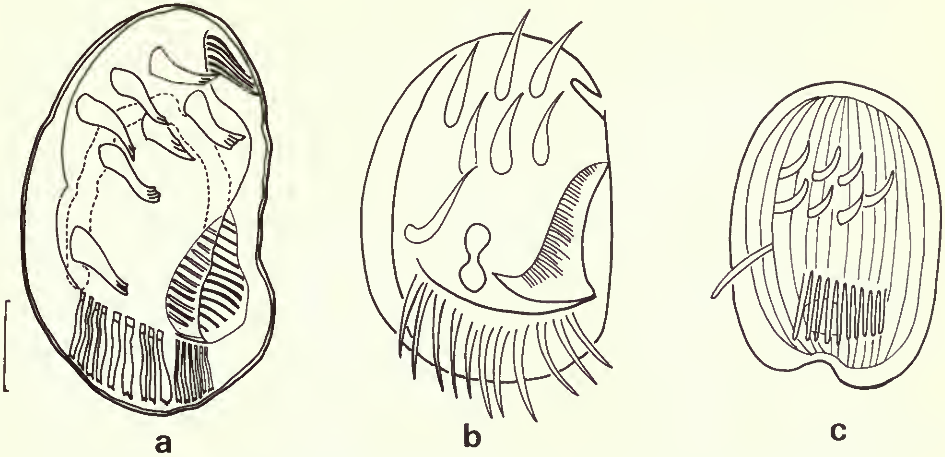

Fig. 16 *Aspidisca polystyla*: (a) after Tuffrau, 1964; (b) after Stein, 1859; (c) after Pereyaslawzewa, 1886 (called *A. plana*).

Aspidisca polystyla Stein, 1859

Aspidisca plana Pereyaslawzewa, 1886

The original study of this species by Stein (1859) was very detailed and he characterised the species by the presence of a large number of transverse cirri. Most of the original specimens had 10–11 transverse cirri but some had 12, up to 15 have been observed in later studies. Plough (1916), Kahl (1932) and Tuffrau (1964) all described the species and Tuffrau mentioned the silver-line system. Dragesco (1963) described an organism which he regarded as *A. polystyla* possessing only five transverse cirri, but the present authors consider this specimen to be *A. steini*.

DIAGNOSIS. *Aspidisca polystyla* (Fig. 16) is a small (40–50 µm) species characterised by 10–15 transverse cirri. The body outline is smooth and the dorsal surface is marked by three longitudinal ridges. The arrangement of the seven frontoventral cirri is diagnostic: two rows of three cirri are found near the anterior while one cirrus is found near the transverse group. There are about 15 membranelles in the posterior AZM and two to six anterior cilia. The macronucleus is horseshoe-shaped but no micronucleus has been observed. The dorsal silver-line system was described by Tuffrau (1964) as consisting of four kineties with hexagonal links as in *Euplotes eurystomus* but no illustration was provided.

Aspidisca major (Madsen, 1931) Kahl, 1932

Onychaspis (*Aspidisca*) *steini* var. *major* Madsen, 1931
Aspidisca steini var. *major* (Madsen, 1931) Kahl, 1932
Aspidisca major var. *faurei* Dragesco, 1960

Madsen (1931) described this species as *Onychaspis* (*Aspidisca*) *steini* var. *major* which was distinguished from *A. steini* Buddenbrock, 1920 by its larger size. The description was brief and there was no mention of nuclei. Kahl (1932) redescribed this species as *Aspidisca* (*Onychaspis*) *steini* var. *major* and listed *Aspidisca major* Madsen (?) with two macronuclei as a separate species.

Kahl separated *A. steini* var. *major* and *A. major* by the difference in number and disposition of the anterior cilia. Tuffrau (1964) later described *A. major* Madsen (?) which is almost identical to the *Onychaspis* (*Aspidisca*) *steini* var. *major* of Madsen (1931) and had two macronuclei. Tuffrau noted that the two macronuclei were connected by a nuclear membrane, and in *A. major* var. *faurei* Dragesco, 1960 they appear to be joined more completely. However, in both cases there are two distinct nuclear elements.

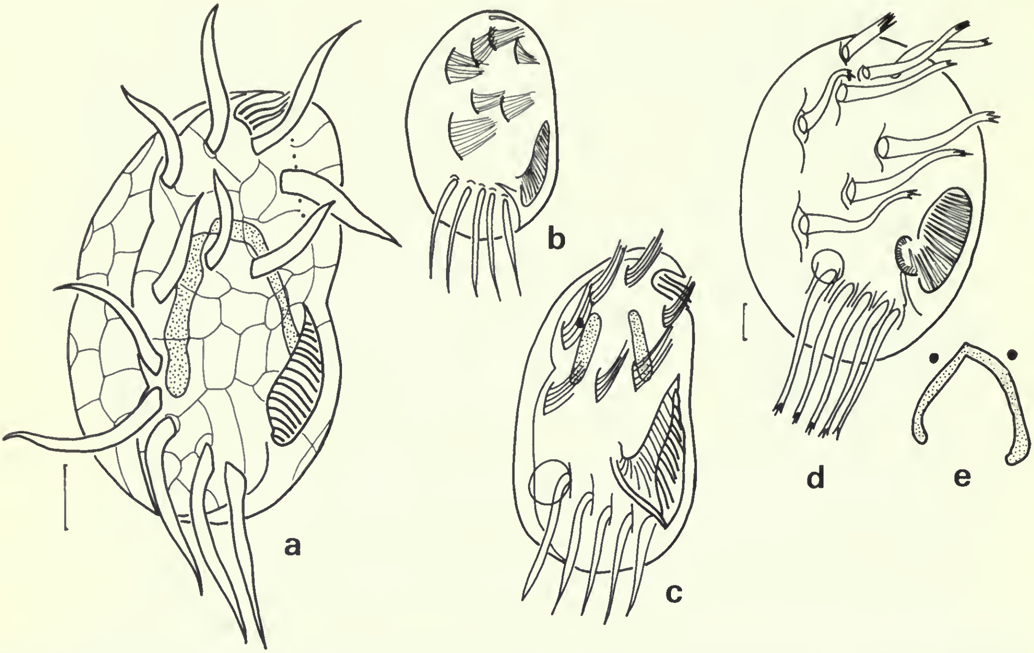

Fig. 17 *Aspidisca major*: (a) after Tuffrau, 1964; (b) after Madsen, 1931 (called *Onychaspis* (*Aspidisca*) *steini* var *major*); (c) after Kahl, 1932; (d) after Dragesco, 1960 (called *A. major* var *faurei*); (e) nuclear features after Dragesco, 1960.

DIAGNOSIS. *Aspidisca major* (Fig. 17) is a medium size (60–100 μm) oval species with perfectly smooth borders and a smooth dorsal surface. The seven frontoventral cirri are in 'polystyla-arrangement' and the five transverse cirri are long. The group of one to four anterior cilia is found just anterior of the II/3 cirrus as in *A. steini*. The peristome, with about 15 membranelles in the posterior AZM, is small relative to the body size. There are two ellipsoid macronuclei which may be connected by a nuclear membrane. The dorsal silver-line system consists of four rows of sensory bristles with transverse links forming regular polygons as in *A. polystyla* and *Euplotes eurystomus* (Tuffrau, 1964).

Aspidisca steini Buddenbrock, 1920

Aspidisca glabra Kahl, 1928
Aspidisca hyalina Dragesco, 1954
[*Aspidisca polystyla* Stein; Dragesco, 1963 Misidentification]

The original specimens of this species were found in a marine aquarium in Germany. Buddenbrock (1920) pointed out the possibility of it being a variety of *A. polystyla* Stein which differs only in having many more transverse cirri. However, it was later found that the two species could be distinquished by their silver-line systems. Kahl (1932) inadequately redescribed the species, but Borror (1963) found an organism of similar shape and ciliature in N. America which he identified as *A. steini* and gave data concerning its size, micronucleus and dorsal kineties for the first time.

Diagnosis. *Aspidisca steini* (Fig. 18) is a small (30–35 µm) species characterised by its smooth outline and smooth dorsal surface. The seven frontoventral cirri are in 'polystyla-arrangement' and the extreme left cirrus of the five transverse cirri may be double-based or split into two making six transverse cirri. There are eight to nine membranelles in the posterior AZM and the anterior ciliary organelle containing two to four cilia is positioned just anterior to the II/3 cirrus. The macronucleus is C-shaped and the spherical micronucleus is located on its left. There are five dorsal kineties carrying, from left to right, 2 : 4 : 5 : 5 : 4 cilia respectively.

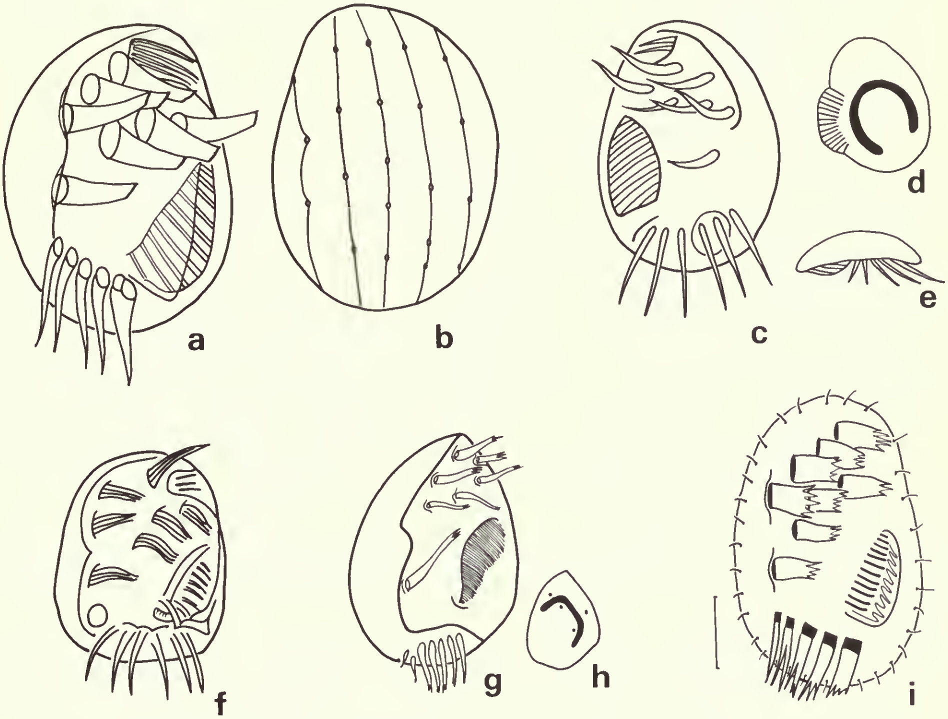

Fig. 18 *Aspidisca steini*: (a & b) ventral surface & dorsal silver-line system after Borror, 1963; (c–e) after Buddenbrock, 1920; (f) after Kahl, 1928 (called *A. glabra*); (g–h) after Dragesco, 1954 (called *A. hyalina*); (i) after Dragesco, 1963 (called *A. polystyla*).

Aspidisca aculeata (Ehrenberg, 1838) Kahl, 1932

Euplotes aculeata Ehrenberg, 1838
Onychaspis aculeata Manseld, 1923

Ehrenberg (1838) first discovered this small species with a dorsal 'backward curving hook' in seawater at Kiel which he called *Euplotes aculeata* Ehrenberg, 1838. The original diagrams were crude and practically identical to those of *Euplotes turritus* Ehrenberg, 1838. Mansfeld (1923) found in an aquarium in Berlin a hypotrich, *Onychaspis aculeata*, with a dorsal thorn similar to *Aspidisca turrita* (Ehrenberg, 1838) Claparède & Lachmann, 1858 but differing in having dorsal ribs as well as a thorn. Kahl later (1932) identified it as *Euplotes aculeata* Ehrenberg and transferred it to the genus *Aspidisca*. Borror (1965) and Agamaliev (1974) redescribed the species in greater detail, stained the silver-line system and noted up to three micronuclei. The arrangement of the frontoventral cirri of *Onychaspis aculeata* illustrated by Mansfeld appears to be different from the two usual patterns but we consider the illustrations by the later authors more reliable.

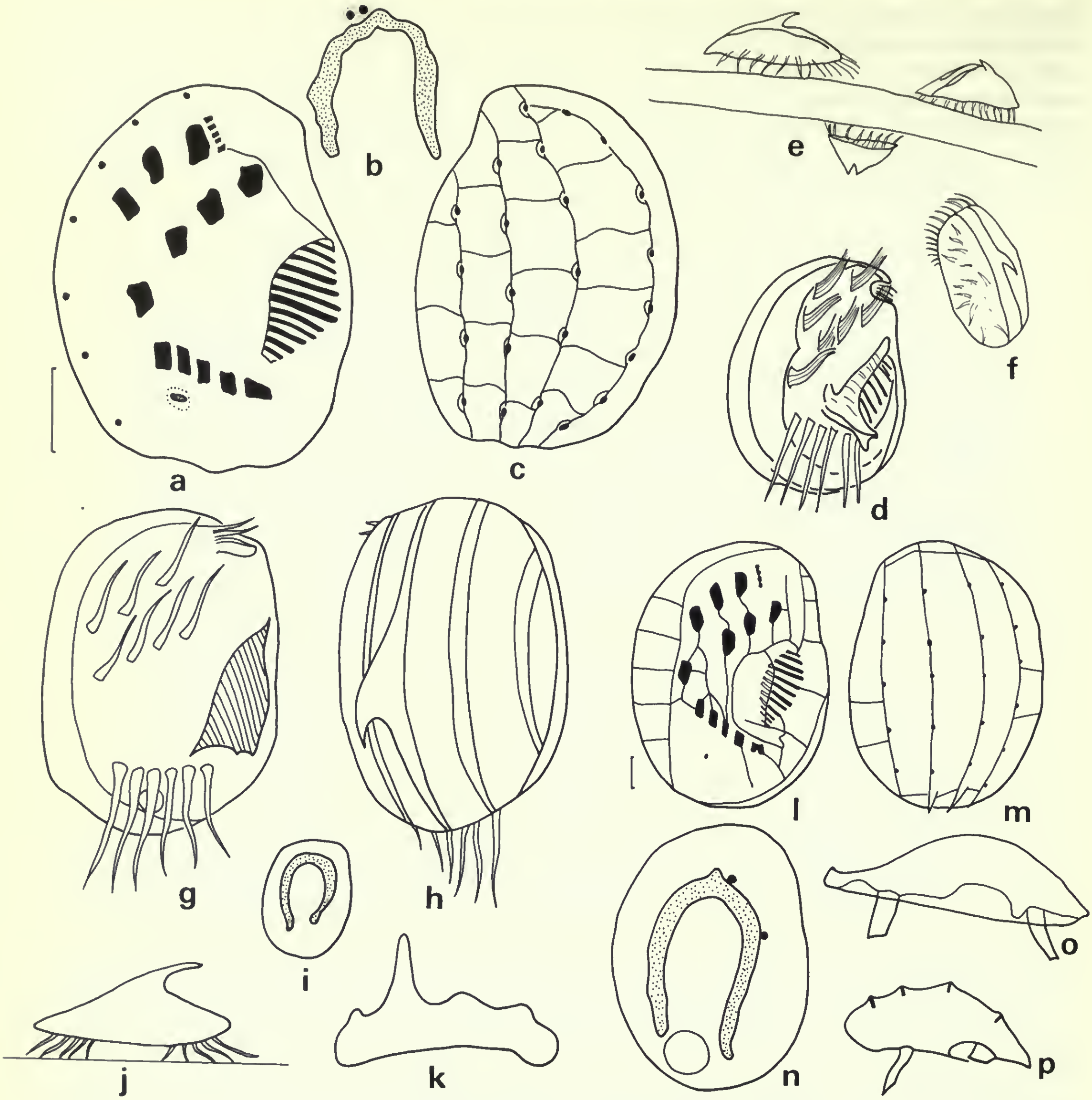

Fig. 19 *Aspidisca aculeata*: (a–c) after Agamaliev, 1974; (d) after Kahl, 1932; (e–f) after Ehrenberg, 1838 (called *Euplotes aculeata*); (g–k) after Mansfeld, 1923 (called *Onychaspis aculeata*); (l–p) after Borror, 1965.

DIAGNOSIS. *Aspidisca aculeata* (Fig. 19) is a small (30–50 µm) species with seven frontoventral cirri in 'polystyla-arrangement' which distinguishes it from *Aspidisca turrita*, and five or six transverse cirri. The body is oval, slightly convex on the right, and the outline is smooth. Dorsally there are four ribs, the second from the left of which carries a thorn. The macronucleus is C-shaped and one to three micronuclei may be found by its anterior left. The peristome is average in size with about ten membranelles in the posterior AZM and there are three to five anterior cilia. The silver-line system, according to Agamaliev (1974), consists of five dorsolateral kineties with single cross-links, and the four dorsal kineties carry, from left to right, 4 : 5 : 6 : 8 cilia respectively; while Borror (1965) found no lateral kineties and the four dorsal kineties carry, from left to right, 5 : 5 : 5 : 6 cilia respectively and a few cross-links were noted.

Aspidisca tuberosa Kahl, 1932

Oxytricha cicada Ehrenberg, 1838
Coccudina costata Dujardin, 1841

The description of this species by Kahl (1932) is brief but the ventral ciliature and the crenated dorsal ribs are clearly illustrated. A small, smooth-bordered hypotrich with crenated ribs was described as *Oxytricha cicada* by Ehrenberg, 1838, and was considered by Dujardin (1841) to be similar to *Coccodina costata*. Since the specific name *cicada* is preoccupied, the correct combination for this taxon should be *Aspidisca costata*. But, due to a long history of misuse of this combination when describing *A. cicada* (Müller, 1786) Claparède & Lachmann, 1858 (see p. 12), the present authors refrain from making this emendation.

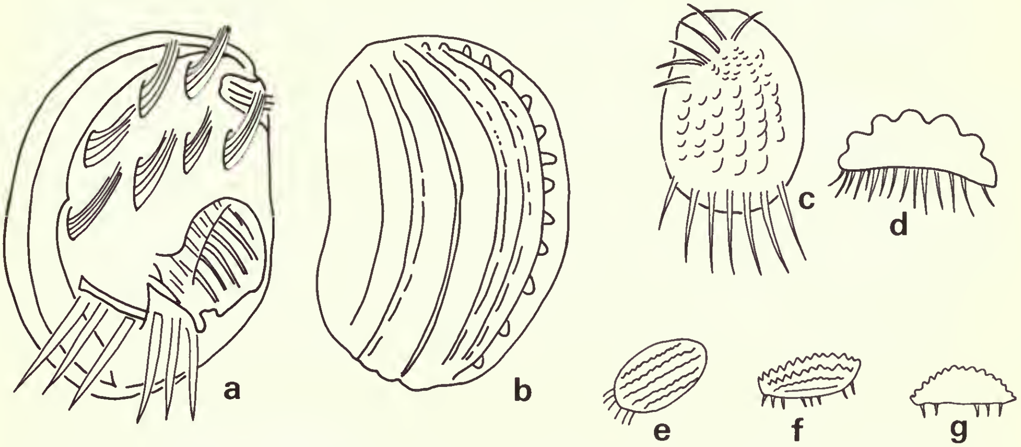

Fig. 20 *Aspidisca tuberosa*: (a–b) after Kahl, 1932; (c–d) after Dujardin, 1841 (called *Coccudina costata*); (e–g) after Ehrenberg, 1838 (called *Oxytricha cicada*).

DIAGNOSIS. *Aspidisca tuberosa* (Fig. 20) is a small (30–35 µm) species characterised by four to six crenated sharp dorsal ribs. Its body shape is typical of the genus, oval and convex on the right. There are seven frontoventral cirri in 'polystyla-arrangement', six transverse cirri, three cilia in the anterior ciliary organelle and ten membranelles in the posterior AZM.

Aspidisca polypoda (Dujardin, 1841) Kahl, 1932

Coccudina polypoda Dujardin, 1841
Aspidisca andreewi Mereschowsky, 1878
Aspidisca polystyla ~~*var*~~ *maxima* Gourret & Roeser, 1886
Aspidisca quadrilineata Kahl, 1932

This species characterised by seven or eight conspicuous dorsal ribs was first described by Dujardin (1841). Kahl (1932) clearly illustrated the dorsal ribs and the ventral cirri of specimens from Heligoland and transferred the species to the genus *Aspidisca*. Dragesco (1960) described somewhat larger organisms from Roscoff which he identified as *A. polypoda* but made no mention of the characteristic dorsal ribs. The latter author also described the nuclei and mentioned that 'le tégument de ce cilié montre une fine structure superficielle, constituant un véritable réseau à mailles fines' but presented no diagrams of these. As in the case of *A. lynceus* and *A. cicada*, a distinctive silver-line system would be a more precise feature for separating *A. polypoda* from *A. steini* rather than just the presence of dorsal ribs.

DIAGNOSIS. *Aspidisca polypoda* (Fig. 21) is a small (30–55 µm) species with seven or eight distinctive dorsal ribs which distinguishes it from *A. steini*, and the 'polystyla-arrangement' of the seven frontoventral cirri distinguishes it from *A. cicada*. Six transverse cirri are generally noted. The peristome is small with 8–15 membranelles in the posterior AZM and there are three to four anterior cilia. The macronucleus is described as a horseshoe-shaped opening towards the posterior right and the spherical micronucleus is found in the opening (Dragesco, 1960).

Aspidisca dentata Kahl, 1928

This species has been described only by Kahl (1928, 1932) and it was found extensively in Oldesloe, Kiel and the North Sea but not in large numbers.

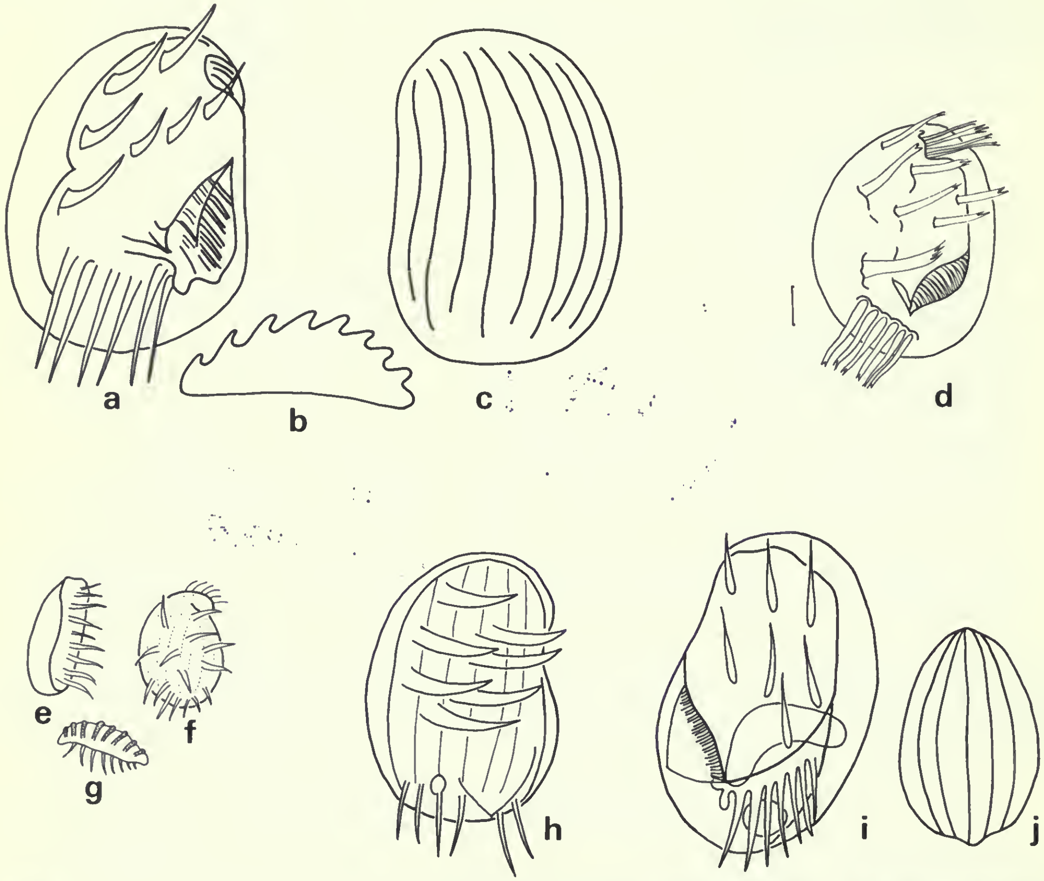

Fig. 21 *Aspidisca polypoda*: (a–c) after Kahl, 1932; (d) after Dragesco, 1960; (e–g) after Dujardin, 1841 (called *Coccudina polypoda*); (h) after Mereschkowsky, 1878 (called *A. andreewi*); (i–j) after Gourret & Roeser, 1886 (called *A. polystyla* var *maxima*).

Diagnosis. *Aspidisca dentata* (Fig. 22) is a small (20–40 µm) species. It has four dorsal ribs, one of which bears a thorn. There are seven frontoventral cirri in 'polystyla-arrangement', six transverse cirri, six to ten membranelles in the posterior AZM and four anterior cilia. The presence of a peristomial spur separate this from the almost identical species *Aspidisca aculeata*.

Aspidisca magna Kahl, 1932

Aspidisca pelvis Delphy, 1938
Aspidisca maxima Vacelet, 1961 (see Vacelet, 1961*b*)

The original description of this species by Kahl (1932) was inadequate as only six to eight specimens were observed. However, its large size is distinctive. Tuffrau (1964) described an equally large

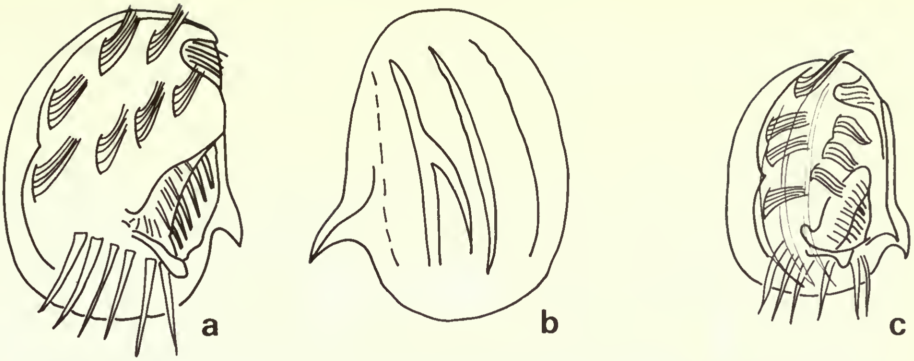

Fig. 22 *Aspidisca dentata*: (a & b) ventral & dorsal surface after Kahl, 1932; (c) ventral surface after Kahl, 1928.

species which also possessed a peristomial spur and this he identified as *A. magna*. Although Tuffrau used silver-impregnation techniques, only a vague description of the dorsal silver-line system was given.

DIAGNOSIS. *Aspidisca magna* (Fig. 23) is the largest (135–157 μm) species described. The body is broadly oval and its outline is broken only by a broad conspicuous peristomial spur. There are four ribs on the dorsal surface and the central ones of these are higher than the lateral ones. The seven frontoventral cirri are in 'polystyla-arrangement' and there are five or six transverse cirri. The peristome is small in proportion to the body size with about 20 membranelles in the posterior

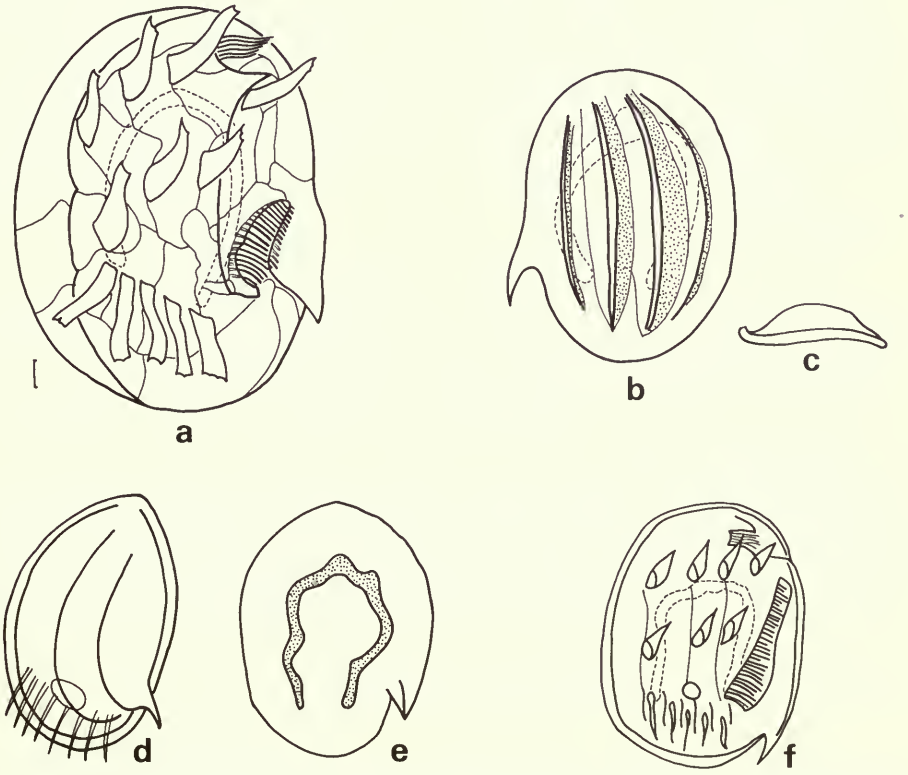

Fig. 23 *Aspidisca magna*: (a) after Tuffrau, 1964; (b–c) after Kahl, 1932; (d–e) after Delphy, 1938 (called *A. pelvis*); (f) after Vacelet, 1961*b* (called *A. maxima*).

AZM and there are six anterior cilia. The macronucleus is a slim horseshoe but no micronucleus has been noted. The dorsal argyrome pattern is described as 'classic' with four kinety meridians joined by simple transverse links (Tuffrau, 1964).

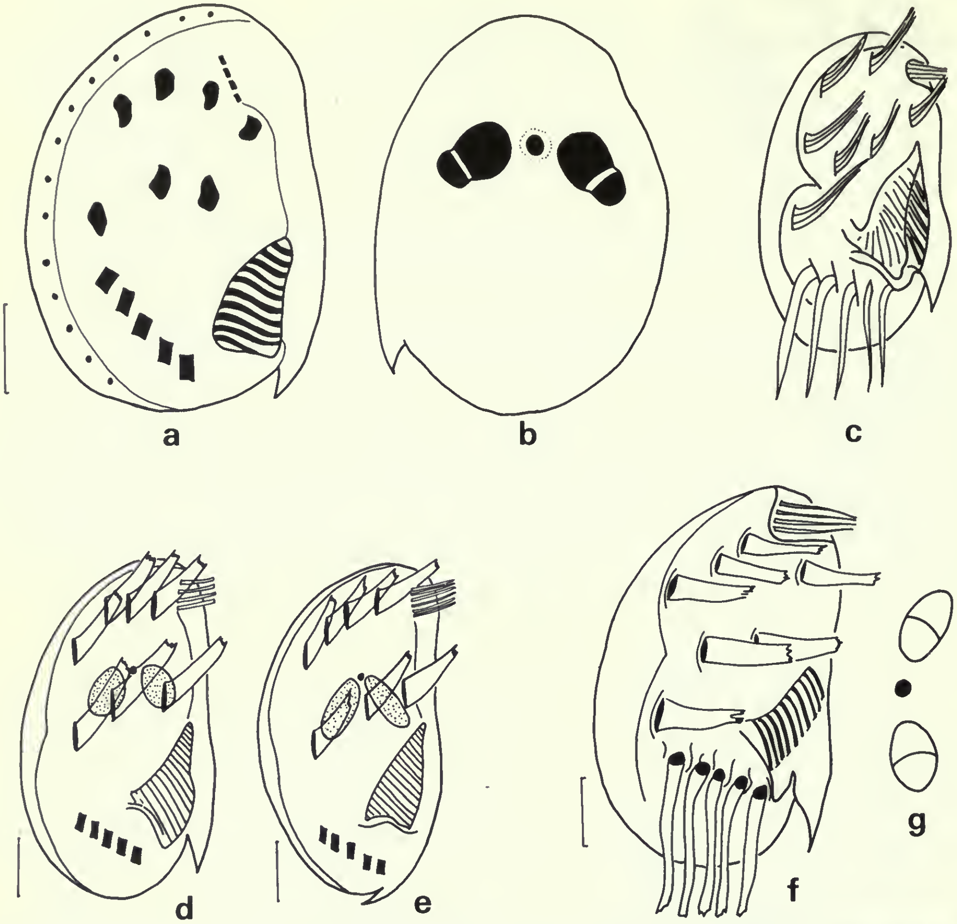

Fig. 24 *Aspidisca fusca*: (a–b) after Agamaliev, 1967; (c) after Kahl, 1932; (d) after Burkovsky, 1970; (e) after Burkovsky, 1970 (called *A. irinae*); (f–g) after Dragesco, 1965.

Aspidisca fusca Kahl, 1928

Aspidisca irinae Burkovsky, 1970

This species was first found in Oldesloe, Kiel. In the original description, Kahl (1928) did not mention the nuclei but Dragesco (1965) identified specimens from Port Etunnie and reported the presence of two macronuclei. Agamaliev (1967) was unsuccessful in silver-impregnating the dorsal argyrome of specimens from the Caspian Sea but successfully stained the ventral cirri and a lateral kinety. Burkovsky (1970) described *A. fusca* with frontoventral cirri in an uncharacteristic arrangement which the present authors would question. In the same paper Burkovsky described a new species *A. irinae* which is practically identical to *A. fusca* and is here regarded as a synonym.

Diagnosis. *Aspidisca fusca* (Fig. 24) is a small to medium size (40–60 µm) species. The body is oval, slightly convex on the right, and the dorsal surface is arched and smooth. There are seven frontoventral cirri in 'polystyla-arrangement' and five transverse cirri. The peristome is small with 10–12 membranelles in the posterior AZM and there are four to six anterior cilia. Two centrally located oval macronuclei are arranged in an inverted 'V' shape with a spherical micronucleus situated between. The prominently developed peristomial spur distinguishes this species from *A. major*.

Aspidisca sedigita Quennerstedt, 1867

Aspidisca hexeris Quennerstedt, 1869
Aspidisca crenata Fabre-Domerque, 1869
Aspidisca angulata Bock, 1952
Aspidisca pertinens Bock, 1955
Aspidisca fjeldi Dragesco, 1960
Aspidisca tridentata Dragesco, 1963
Aspidisca caspica Agamaliev, 1967
Aspidisca fuscoides Agamaliev, 1975

Aspidisca sedigita is in almost every respect like *Aspidisca leptaspis* described by Fresenius two years earlier, but the absence of a VI/2 cirrus distinguishes *A. sedigita* from the earlier species. The four species *A. hexeris*, *A. crenata*, *A. pertinens* and *A. fjeldi* are all of similar size, shape and ciliature to *A. sedigita* but have been designated as separate species since they have only one or no projection on the left border other than the peristomial spur. As we do not consider lateral projections to be stable taxonomic features the above listed species are regarded as synonyms of *A. sedigita*. The two species *A. tridentata* and *A. caspica* both have three dentations on the left border are undoubtedly identical to *A. sedigita*.

DIAGNOSIS. *Aspidisca sedigita* (Fig. 25) is a medium size (50–100 µm) species. Its shape is typical of the genus, oval and convex on the right. On the left border is a prominent peristomial spur and one or two smaller projections. The posterior border may be serrated and the dorsal surface is marked by two to four grooves. There are seven frontoventral cirri in 'polystyla-arrangement' and six to seven transverse cirri. The peristome is of average size and there are four to eight anterior cilia. The macronucleus is horseshoe-shaped and up to three micronuclei have been observed. According to the description of *A. caspica* by Agamaliev (1967, 1970), the silver-line system consists of five dorsolateral kineties carrying a variable number of cilia and the argyrome pattern is also variable.

Aspidisca orthopogon Deroux & Tuffrau, 1965

This species has been described only by Deroux & Tuffrau (1965) who gave a detailed account of the morphogenesis of the ventral ciliature.

DIAGNOSIS. *Aspidisca orthopogon* (Fig. 26) is one of the few larger (80–110 µm) species of the genus. Its outline is smooth and the body a perfect oval without being convex on the right, as is typical of the genus. Other than seven frontoventral cirri in 'polystyla-arrangement', it has a satellite-like V/3 cirrus (also named 'cirre surnuméraire' by Deroux & Tuffrau, 1965) and not the VI/2 cirrus found in the other species with eight frontoventral cirri. Its peristome with 40–50 membranelles in the posterior AZM is uniquely extensive and there are four anterior cilia. The macronucleus is a classic horseshoe and the micronucleus is by its anterior left. The silver-line system consists of four symmetrically aligned dorsal kineties each carrying more than 30 cilia, and simple transverse links forming a 'draught-board' pattern.

Aspidisca leptaspis Fresenius, 1865

Aspidisca psammobiotica Burkovsky, 1970
[*Aspidisca lyncaster* Stein; Kahl, 1932 Misidentification]
[*Aspidisca lyncaster* Stein; Dragesco, 1960 Misidentification]
[*Aspidisca lyncaster* Stein; Tuffrau, 1964 Misidentification]

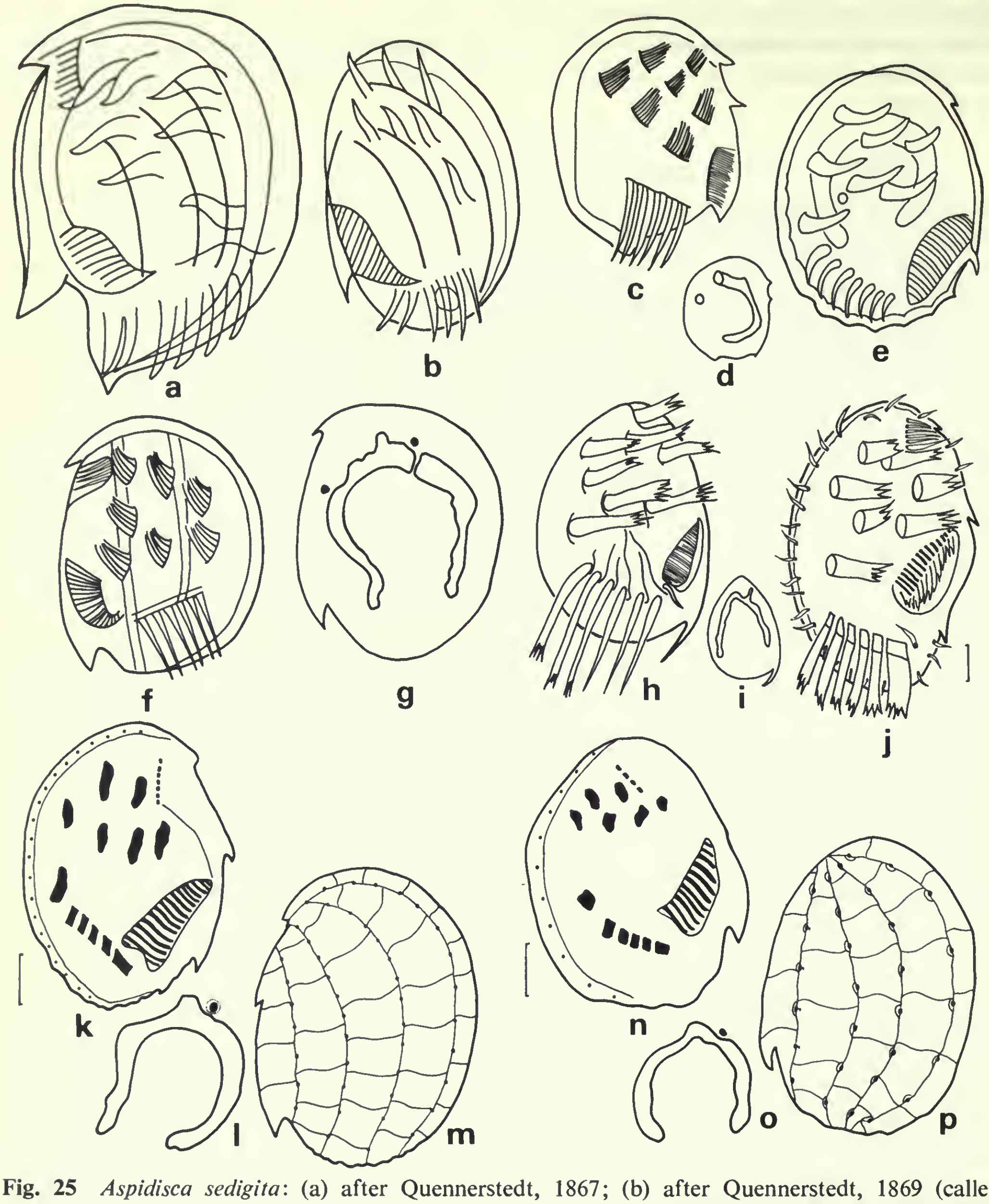

Fig. 25 *Aspidisca sedigita*: (a) after Quennerstedt, 1867; (b) after Quennerstedt, 1869 (called *A. hexeris*); (c–d) after Bock, 1952 (called *A. angulata*); (e) after Fabre-Domerque, 1885 (called *A. crenata*); (f–g) after Bock, 1955 (called *A. pertinens*); (h–i) after Dragesco, 1960 (called *A. fjeldi*); (j) after Dragesco, 1963 (called *A. tridentata*); (k–m) after Agamaliev, 1967 (called *A. caspica*); (n–p) after Agamaliev, 1975 (called *A. fuscoides*).

[*Aspidisca sedigita* Quennerstedt; Kahl, 1932 Misidentification]
[*Aspidisca sedigita* Quennerstedt; Dragesco, 1960 Misidentification]

Fresenius (1865) found a large and a small (30–35 µm) *Aspidisca* in a seawater acquarium. He stated that the former was similar to *A. lyncaster* and described the latter as *A. leptaspis*. Since Kahl (1932) found large specimens of the latter species, it is likely that Fresenius described two different size groups of the same species. There are eight frontoventral cirri illustrated in Fresenius's diagram which we consider are a major diagnostic feature. Two species, *A. lyncaster* (Muller) Stein and *A. sedigita* Quennerstedt, have been described with similar ciliature but only seven frontoventral cirri. Tuffrau (1964) described the silver-line system of what he identified as *A. lyncaster* but with eight frontoventral cirri and it is similar to that of *A. leptaspis* illustrated by Agamaliev (1974).

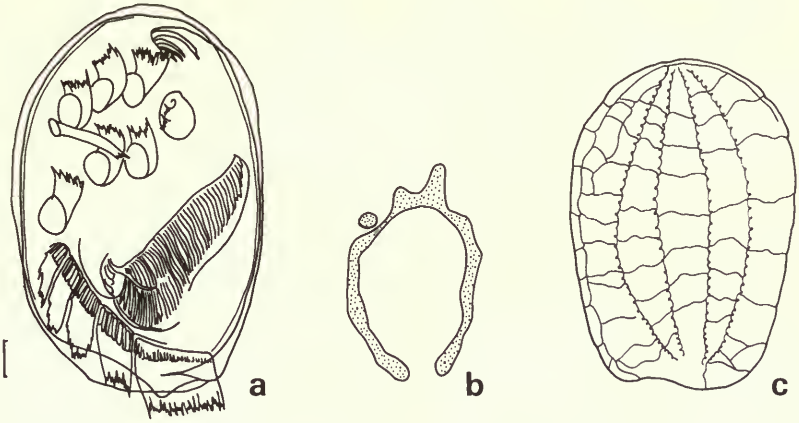

Fig. 26 *Aspidisca orthopogon*: (a) ventral ciliature; (b) nuclei; (c) dorsal silver-line system (after Deroux & Tuffrau, 1965).

DIAGNOSIS. *Aspidisca leptaspis* (Fig. 27) is a small to medium size (30–90 µm) species. It is characterised by the presence of a prominent peristomial spur and a satellite-like VI/2 cirrus which together with seven other frontoventral cirri in 'polystyla-arrangement' make a total of eight. One or two small dentations may be found at the anterior left and serrations on the posterior border. There are five or six transverse cirri and three or four dorsal ribs. The peristome is fairly extensive accommodating about 15 membranelles in the posterior AZM and the anterior ciliary organelle consists of six to eight cilia. The macronucleus is a perfect horseshoe and two micronuclei have been seen. The silver-line system is of five dorsolateral kineties, the dorsal kinety on the extreme right hand runs along the border and joins the two central kineties anteriorly. Simple transverse links join the kineties. The longest dorsal kinety on the right carries about 20 cilia (see Agamaliev, 1974).

Aspidisca pulcherrima Kahl, 1932

Aspidisca pulcherrima var. *baltica* Kahl, 1932
Aspidisca baltica Borror, 1965

This species was originally described from the North Sea by Kahl (1932). Tuffrau (1964) identified this species from Roscoff and described its silver-line system but did not mention any crenated dorsal ribs which is a distinctive feature described by Kahl (1932). Kahl (1932) also described a variety, *A. pulcherrima* var. *baltica*, on the seaweed *Ulva* in the Baltic Sea which he considered had a less serrated posterior border and the dorsal ribs bore 'humps' rather than 'teeth'. Borror (1965) redescribed this variety and raised it to species level for similar reasons, noting that it also had a distinct configuration of the 'right lip of the buccal cavity' and ventral argyromes. Since we do not consider these features as diagnostic characters this variety is treated as a synonym. Borror (1965) also illustrated the silver-line system which agrees with that given by Tuffrau (1964).

DIAGNOSIS. *Aspidisca pulcherrima* (Fig. 28) is a medium size (70–90 µm) species characterised by four crenated dorsal ribs and a rugged body outline. Apart from a prominent peristomial spur, there may be two smaller projections on the anterior left border. Along the posterior border are

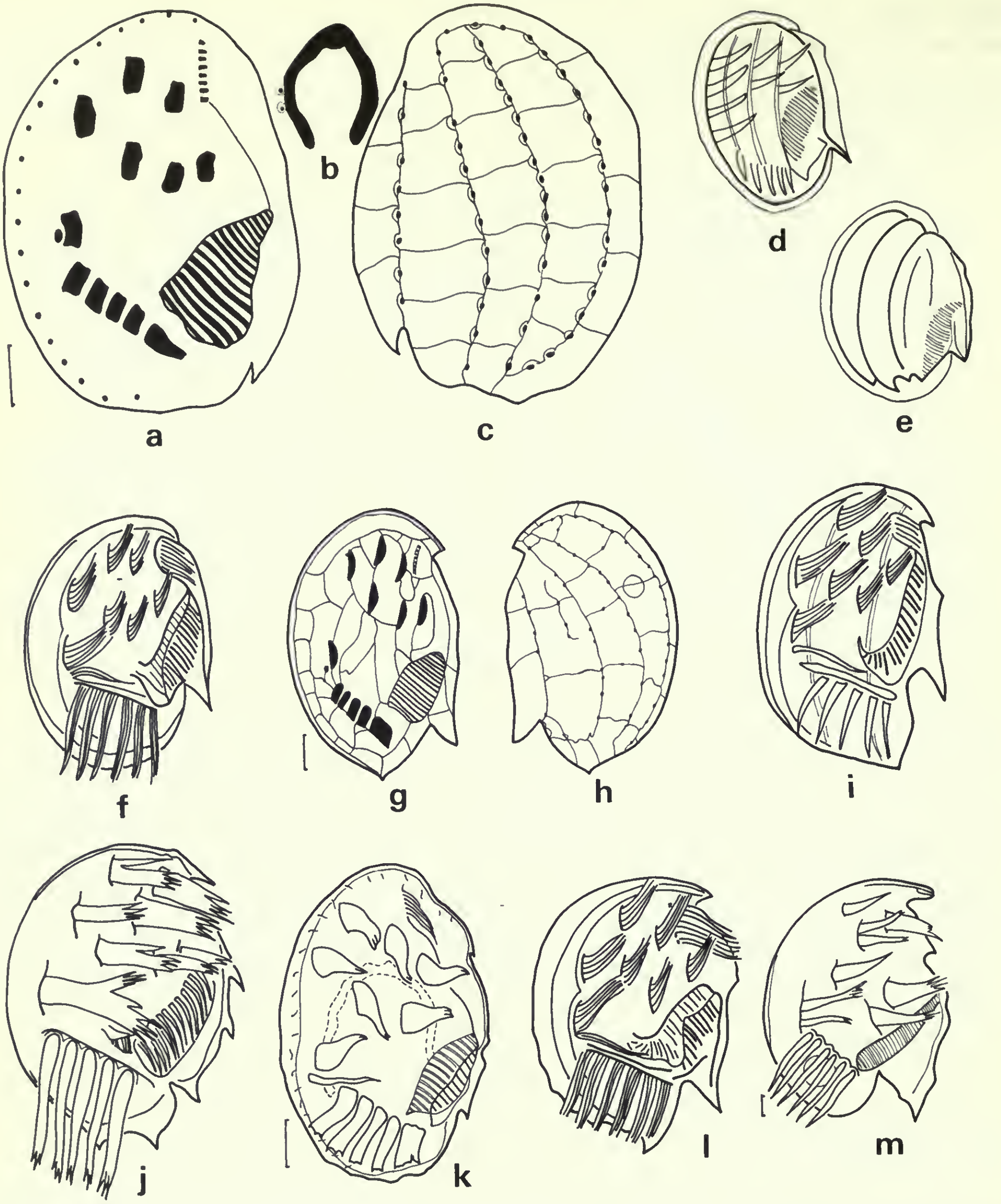

Fig. 27 *Aspidisca leptaspis:* (a–c) after Agamaliev, 1974; (d–e) after Fresenius, 1865; (f) after Kahl, 1932; (g–h) after Burkovsky, 1970 (called *A. psammobiotica*); (i) after Kahl, 1932 (called *A. lyncaster*); (j) after Dragesco, 1960 (called *A. lyncaster*); (k) after Tuffrau, 1964 (called *A. lyncaster*); (l) after Kahl, 1932 (called *A. sedigita*); (m) after Dragesco, 1960 (called *A. sedigita*).

three to four pronounced dentations and the posterior half of the right border is also slightly serrated. There are six or seven transverse cirri and seven frontoventral cirri in 'polystyla-arrangement' plus a satellite-like VI/2 cirrus making eight in all. The macronucleus is C-shaped with one or two micronuclei at its immediate left. There are 15–20 membranelles in the posterior AZM and four to eight anterior cilia. The silver-line system consists of four kinety meridians and simple irregular transverse links.

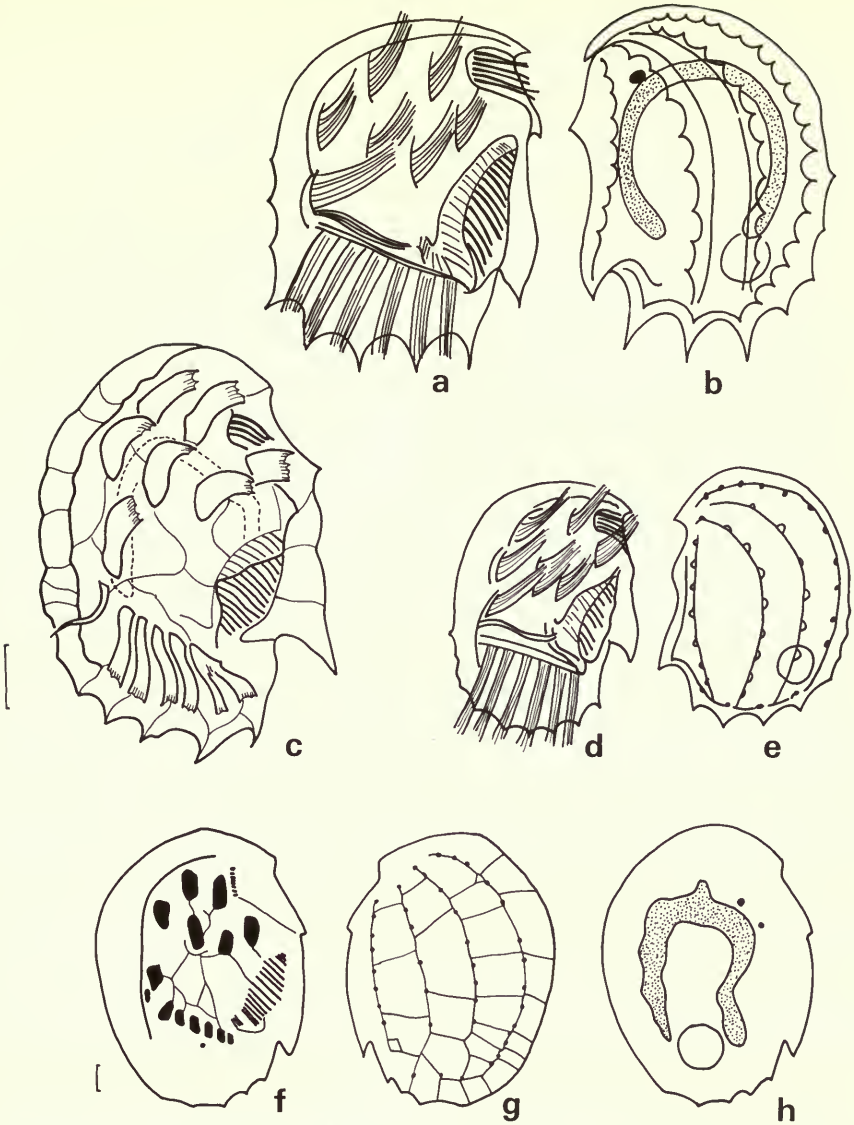

Fig. 28 *Aspidisca pulcherrima*: (a–b) after Kahl, 1932; (c) after Tuffrau, 1964; (d–e) after Kahl, 1932 (called *A. pulcherrima* var *baltica*); (f–h) after Borror, 1965 (called *A. baltica*).

Section C

Key to species with more than eight frontoventral cirri

1 a 11–15 frontoventral cirri and a keel-like dorsal spine . . . . . . ***A. mutans***
b 9 frontoventral cirri and 2 macronuclei . . . . ***A. binucleata***

Aspidisca mutans Kahl, 1932

The large number of cirri on the ventral surface and the keel-like dorsal spine of *A. mutans* are unique to the genus. The description of this species from Kiel is the only source of information.

DIAGNOSIS. *Aspidisca mutans* (Fig. 29) is a large (90–150 µm) species. The oval body is convex on the right and the outline is smooth. It has 11–15 frontoventral cirri aligned in two rows each

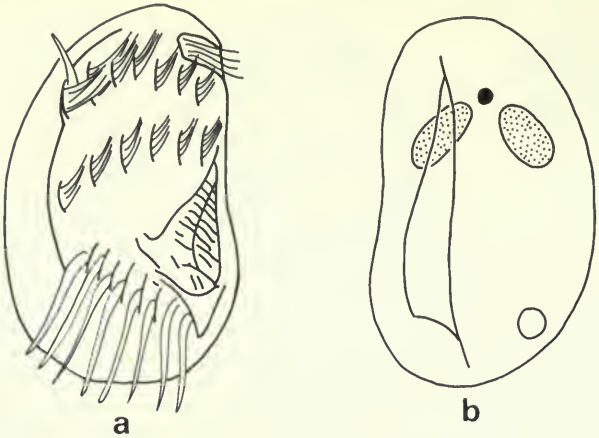

Fig. 29 *Aspidisca mutans*: (a) ventral surface; (b) dorsal surface; (after Kahl, 1932).

with five to seven, and six to eight cirri. A satellite-like cirrus by the anterior right border and seven to eight transverse cirri make a total of up to 24 cirri on the ventral surface. The two oval macronuclei are small and are located anteriorly. The micronucleus is at the apex of the inverted 'V' formed by the macronuclei. There is a keel-like spine dorsally which may 'vary in its acuteness but is seldom absent'.

Aspidisca binucleata Kahl, 1932

The description of this species by Kahl is brief. *A. binucleata* differs from *A. major* only in having nine frontoventral cirri instead of seven.

DIAGNOSIS. *Aspidisca binucleata* (Fig. 30) is a medium size (70–90 μm) species and the outline of the oval body is smooth. There are nine frontoventral cirri, six transverse cirri, 15–20 membranelles in the posterior AZM and four anterior cilia. The two small round macronuclei and a micronucleus on their right are found in the anterior half of the body.

Doubtful species

Aspidisca caudata Vacelet, 1961

This species (Fig. 31) found at the marine station of Endorome-Marseille is 50–65 μm long. There are two dentations on the left border, seven frontoventral cirri in 'polystyla-arrangement', five

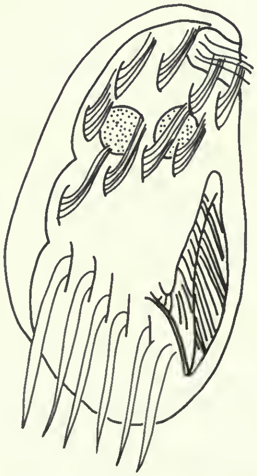

Fig. 30 *Aspidisca binucleata* after Kahl, 1932.

transverse cirri and a horseshoe macronulceus which are diagnostic features of *A. sedigita.* Vacelet (1961*a*) noted a tail-like structure which did not function as a flagellum nor as a cilium but trailed behind, and sometimes the animal seemed to be attached to the substrate by this 'tail'. Vacelet stated, however, that the rare individuals were briefly seen once on the surface of a sediment sample, therefore the present authors are reluctant to regard this as a distinct species until further confirmation and information on this tail-like structure become available.

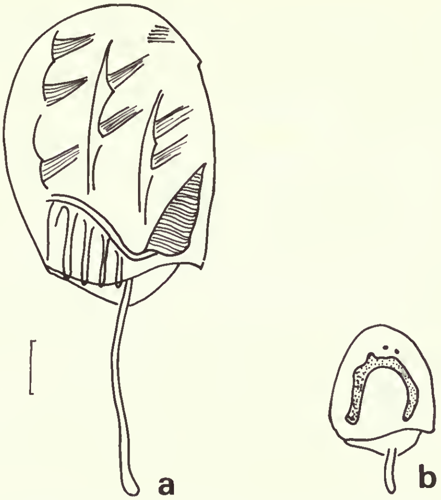

Fig. 31 *Aspidisca caudata*: (a) ventral surface; (b) nuclei (after Vacelet, 1961*a*).

Nomena nuda

Aspidisca bipartita Gourret & Roeser, 1886
Aspidisca denticulata Ehrenberg, 1838
Aspidisca pulvinata Fromentel, 1874
Aspidisca radiata Fromentel, 1874
Aspidisca robusta Kahl, 1932

Appendix 1

Plough's key for identification of the species of *Aspidisca* (Plough, 1916)

A.	Right and left border smooth	a
B.	Left border incised to form a single backwardly directed spur in the posterior third	***A. hexeris***
C.	Left border with two spurs, one in the anterior and one in the posterior third	c
D.	Left border with three spurs	***A. sedigita***
a.	Dorsal surface with recurved thorn-like appendage	***A. turrita****
	Dorsal surface without thorn	a'
c.	Dorsal surface and posterior border serrated	***A. leptaspis***
	Dorsal surface smooth	***A. lyncaster***
a'	Ventral plate projecting beyond left border of carapace	***A. costata****
	Ventral plate not projecting	a''
a''	Peristome reaching anterior border, anal cirri five	***A. lynceus***
	Peristomial cilia not reaching anterior border, anal cirri more than five	***A. polystyla***

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* Indicates the only forms so far reported in freshwater.

Appendix 2

Kahl's key for the identification of species of *Aspidisca* (translated from Kahl, 1932)

1(14)	Freshwater, always with five transverse cirri	2
2 (5)	Transverse cirri in an oblique row at or near the posterior border	3
3 (4)	Transverse cirri at posterior border, only five ventral cirri.	***Aspidiscopsis bengalensis***
4 (3)	Transverse cirri near posterior border, dorsal with four delicate streaks	***A. marsupialis***
5 (2)	Transverse cirri far from the posterior border, the three right transverse cirri are on a ledge	6
6 (9)	The two left transverse cirri are divided at their base by a prominent spike.	7
7 (8)	Dorsal entirely smooth, without ribs and thorns	***A. lynceus***
8 (7)	Dorsal with a thorn arched towards the posterior, the remain surface flat or with delicated longitudinal ribs	***A. turrita***
9 (6)	The two left transverse cirri are not divided by a spike	10
10(11)	Ventral plate forms a tooth on the left, dorsally there are four ribs, of these, the second from the left almost always bears a thorn.	***A. herbicola***
11(10)	Ventral plate without tooth on the left, no thorn dorsally but there are three to six ribs	12
12(13)	Small, almost always strongly arched form with six dorsal ribs	***A. costata***
13(12)	Somewhat larger species with three tall dorsal ribs	***A. sulcata***
14 (1)	Marine species, almost always with six transverse cirri	15
15(34)	No teeth on the left of peristome (one species with five transverse cirri exhibit a tooth adjacent to the flattened side)	16
16(19)	Five transverse cirri	17
17(18)	Next to the peristome on the left, one finds turning of the body, nevertheless, the tooth lies visible	***A. fusca***
18(17)	No lateral tooth next to the peristome	***A. major*** ***A. steini* var. *major***
19(16)	More than five transverse cirri	20
20(33)	Six transverse cirri	21
21(22)	Moderately large flat form with two rounded nuclei (also uncoloured towards the rim) and nine frontoventral cirri	***A. binucleata***
22(21)	Small differently shaped species, always with seven ventral cirri.	23
23(24)	Dorsally are four ribs varying in height, the second from the left of these is almost always long, it bears a very variable thorn	***A. aculeata***
24(23)	Dorsal without thorn, entirely flat or with ribs	25
25(26)	Dorsal flat	***A. steini***
26(25)	Dorsal with ribs	27
27(28)	Dorsal surface strongly arched, with eight clearly marked ribs, posterior edge of the peristome has projection directed back	***A. polypoda***
28(27)	Flattened, with five to six weak ribs	29
29(30)	The peristomial deck forms a prominent triangle	***A. andreewi***

30(29) The posterior edge of the peristome forms a short blunt tooth, this projects back towards the two left transverse cirri 31

31(32) The four (or six) lower but sharply drawn ribs bear at regular intervals, small humps . . . . ***A. tuberosa***

32(31) The four ribs have no humps, sometimes the left rib is not discernible . . . . ***A. quadrilineata***

33(20) Seven to twelve transverse cirri 33a

33a(33b) Seven, eight or nine transverse cirri and always in same proportion with 11, 13 or 15 ventral cirri . . . . . . ***A. mutans***

33b(33a) 10 to 12 transverse cirri but only seven ventral cirri . . . ***A. polystyla***

34(15) On the left of the peristome, the left border bears a broad horizontal tooth. The following species (perhaps with name *A. dentata*) form a distinct subgroup of the genus distinguished by the five to seven relatively short broad transverse cirri inserted obliquely, also the seven ventral cirri are conspicuously broad, frequently at the posterior of the ventral cirri stands a slender side-cirrus lying alongside the transverse ledge 35

35(36) Small form, from a dorsal ridge, a thorn arches towards the posterior . . . . ***A. dentata***

36(35) Dorsal without thorn 37

37(46) The anterior border has an obvious tooth and from there the left side of the nucleus begins (cf. *A. robusta*) 38

38(43) Six transverse cirri, a side-cirrus at the posterior of the ventral cirri, a tooth-like projection at the anterior third on the left border, the right edge is very flat and transparent, in the frontal group there are six to eight membranelles 39

39(42) The posterior border has four to five teeth 40

40(41) The posterior has four or five sharply pointed teeth, dorsally are four high ribs with sharp teeth . . . . . . ***A. pulcherrima***

41(40) The posterior teeth weakly developed, can also be distinct, dorsal ribs low, bear only humps . . . . . ***A. pulcherrima* var *baltica***

42(39) The posterior border shows a tooth only on its left edge and is only very weak in the remainder, dorsally are four variably clear low ribs, often only the two middle one are strongly developed . . . . ***A. sedigita***

43(38) Five or seven transverse cirri. 44

44(45) Five transverse cirri otherwise like the preceeding species . . ***A. lyncaster***

45(44) Seven transverse cirri, the posterior edge either without distinct teeth or weekly notched . . . . ***A. crenata***

46(37) The front left edge forms no distinct tooth, on the left side of the body is without distinct break or with a small indentation 47

47(50) Dorsal ridges weakly indicated 48

48(49) Large flat transparent species with three or four weakly indicated ridges, tooth on the left border exists strongly . . . . ***A. leptaspis***

49(48) Small slender form with a weak tooth on the left border . . ***A. hexeris***

50(47) Four or six strong ribs dorsally 51

51(52) Medium size form, with six to seven uniformly high and strong but round ribs . . . . *A. robusta*

52(51) Very large form with two medial wing-like and two low lateral dorsal ribs . . . . *A. magna*

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The Hemiuroidea : terminology, systematics and evolution

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Synopsis

The history of the classification of the Hemiuroidea and the features which have been used as criteria for distinguishing the higher taxa, such as adult morphology, life-cycle patterns and cercarial anatomy, are discussed. It is suggested that the best basic criterion currently available is the functional morphology of the adult.

Explanations of the terminology with comments on the systematic significance and possible function of the features used in the study of hemiuroid taxonomy are included.

A classification of the Hemiuroidea is presented with keys and definitions of the taxa to the generic level. The classification and definitions are based, where possible, on original observations of sectioned material. The Hemiuroidea is divided into fourteen families. The Accacoeliidae contains the Accacoeliinae and Paraccacladiinae, the latter subfamily consisting of only one genus. The Azygiidae consists of two subfamilies, the Azygiinae and Leuceruthrinae. The Bathycotylidae, Isoparorchiidae and Ptychogonimidae contain single genera, while the Hirudinellidae contains three monotypic genera. The Bunocotylidae is

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redefined and contains the Bunocotylinae, Aphanurinae, Opisthadeninae (including *Neotheletrum* gen. nov.) and Theletrinae subfam. nov. The Derogenidae is also redefined and contains the Derogeninae, Gonocercinae and Halipeginae. The hemiuroids from the teleost swim-bladder, with the exception of *Isoparorchis*, are placed in the Dictysarcidae, which is composed of the Dictysarcinae, Albulatrematinae and Cylindrorchiinae subfam. inq. The Hemiuridae is restricted to ecsomate forms and contains the following subfamilies: Hemiurinae, Dinurinae, Elytrophallinae, Glomericirrinae, Hypohepaticolinae, Lecithochiriinae, Lethadeninae, Plerurinae subfam. nov. and Pulmoverminae. The Lecithasteridae is redefined and is composed of the Lecithasterinae, Hysterolecithinae (including *Thulinia* gen. nov.), Macradeninae, Prolecithinae, Quadrifoliovariinae and Trifoliovariinae. The Sclerodistomidae contains the Sclerodistominae, Prosogonotrematinae and Prosorchiinae. The Sclerodistomoididae fam. nov. is erected for *Sclerodistomoides*, and in the Syncoeliidae, the Syncoeliinae and Otiotrematinae are redefined. An index to the generic names used in this classification is included.

The criteria which may be used as indicators of the relative 'primitiveness' of various taxa or to illustrate phylogenetic relationships within the group are discussed. In relation to this, evolutionary trends within three organ-systems, (1) the seminal storage and disposal apparatus in the female reproductive system, (2) the vitellarium and (3) the terminal genitalia, are studied in detail. Using evidence from this study, an evolutionary picture for the Hemiuroidea is presented, and its relationships with the Didymozooidea and the Paramphistomoidea are commented upon.

I. Introduction

The superfamily Hemiuroidea Looss, 1899, is a group within the Digenea which includes species usually parasitic in the gut, particularly in the stomach, of fishes. They are found predominantly in marine teleosts, but also occur in freshwater teleosts, elasmobranchs and occasionally in amphibians and reptiles. It is not unusual for progenetic forms to occur in molluscs and other marine, and occasionally freshwater, invertebrates. In addition to the alimentary canal of fishes, examples are known from the gall-bladder, swim-bladder, body-cavity, mouth, gills and from the skin, whilst all known species of one group are found in the lung of sea-snakes. Overall, the hemiuroids form a very diverse group, not only in habitat, but also in morphology. Indeed, the wide variations in adult morphology, even within proposed higher taxa, have resulted in a good deal of confusion with regard to the validity, composition and systematic relationships of these taxa.

The superfamily was erected, under the name Hemiurida, by Dollfus (1923), and comprised the families Hemiuridae, Accacoeliidae and Syncoeliidae. Prior to this Looss (1907, 1908) had carefully re-described many species of hemiuroids and set a basic pattern on which later authors, notably Odhner (1911), Poche (1926) and Führmann (1928), were able to build. These early workers based their classifications entirely upon adult morphology and divided the group into a small number of families, although not always indicating the relationships between these families. Odhner (1911), for example, grouped three families together, the Hemiuridae, Azygiidae and Didymozoidae. Since Odhner, the concept of the Hemiuridae has been sub-divided, condensed and sub-divided again on numerous occasions. Systematic histories of the Hemiuroidea have been compiled by Chauhan (1954), Skrjabin & Guschanskaja (1954, 1956, 1960) and more recently by Stunkard (1973), although the latter author has omitted the important contributions of Chauhan (1954), Manter & Pritchard (1960*a*) and Mehra (1962). In order to avoid repetition, we have condensed several of the more recent conceptions of the Hemiuroidea in the form of Table 1. It can be seen from this table that Odhner's original conception was split by Yamaguti (1971) into three superfamilies and eighteen families, one of which, the Hemiuridae, contains twenty-five subfamilies. The large number of higher taxa in this rather uncritical work of Yamaguti appears to be the result of the acceptance of inadequate descriptions as being accurate. Stunkard (1973) summarized the problem succinctly as follows: 'in the course of the past hundred years, a large number of trematodes have been described, many on inadequate and erroneous information and based often on a single specimen. New genera and higher taxonomic categories have been erected to receive these dubious species.' Yamaguti, for example, has accepted three genera in three different families for forms which we consider to be synonymous with the genus *Elongoparorchis* Rao, 1961.

Recent conceptions of the Hemiuroidea, and of the Digenea in general, have been greatly

Table 1 Some recent classifications of the Hemiuroidea

Present classification	La Rue (1957)	Skrjabin & Guschanskaja (1956; 1958; 1960)	Manter & Pritchard (1960*a*)	Mehra (1962)	Yamaguti (1971)
	Hemiurata	**Hemiurata** (1960)			
HEMIUROIDEA	**HEMIUROIDEA**	**HEMIUROIDEA**	**HEMIUROIDEA**	**HEMIUROIDEA**	**HEMIUROIDEA**
Accacoeliidae	Bathycotylidae	Accacoeliidae	Accacoeliidae	Accacoeliidae	Bathycotylidae
Azygiidae	Didymozoidae	Aerobiotrematidae	Aerobiotrematidae	Arnolidae	Botulidae
Bathycotylidae	Dinuridae	Bathycotylidae	Didymozoidae	Bathycotylidae	Hemiuridae
Bunocotylidae	Halipegidae	Dinuridae	Hemiuridae	Hemiuridae	Hirudinellidae
Derogenidae	Hemiuridae	Elytrophallidae	Hirudinellidae	Hirudinellidae	Lampritrematidae
Dictysarcidae	Isoparorchiidae	Halipegidae	Isoparorchiidae	Isoparorchiidae	Mabiaramidae
Hemiuridae	Lecithasteridae	Haplosplanchnidae	Prosogonotrematidae	Lampritrematidae	Prosogonotrematidae
Hirudinellidae	Lecithochiriidae	Hemiuridae	Syncoeliidae	Oesophagicolidae	Ptychogonimidae
Isoparorchiidae	Ptychogonimidae	Isoparorchiidae		Prosogonotrematidae	Sclerodistomidae
Lecithasteridae		Lampritrematidae	**'Azygiata'**	Ptychogonimidae	
Ptychogonimidae	**Azygiata**	Lecithasteriidae	Azygiidae	Sclerodistomidae	**ACCACOELIOIDEA**
Sclerodistomidae	**AZYGIOIDEA**	Lecithochiriidae	Ptychogonimidae	Syncoeliidae	Accacoeliidae
Sclerodistomoididae	Azygiidae	Ptychogonimidae		(Families not considered to be hemiuroid are not dealt with)	
Syncoeliidae	Bivesiculidae	Sclerodistomidae			**ISOPARORCHIOIDEA**
		Syncoeliidae			Aerobiotrematidae
	TRANSVERSOTREMATOIDEA				Albulatrematidae
	Transversotrematidae	**Azygiata** (1958)			Cylindrorchiidae
	(Some families omitted due to lack of information on life-history)	**AZYGIOIDEA***			Dictysarcidae
		Azygiidae			Isoparorchiidae
		Hirudinellidae			Pelorohelminthidae
		Liocercidae			Tetrasteridae
		Xenoperidae			
		? **SUPERFAMILY**			? **SUPERFAMILY**
		Aphanhysteridae			Azygiidae
		Botulidae			? Aphanhysteridae
		Prosthogonotrematidae			Syncoeliidae (related to Hemiuridae)

* 1956 – included in Hemiurata.

influenced by the work of La Rue (1957), who sub-divided the Digenea into two groups, the Epitheliocystidia and the Anepitheliocystidia, depending upon the epithelial or membranous nature of the lining of the cercarial excretory vesicle. The Azygiidae was placed in the latter group, while the remainder of the hemiuroids with 'known' life-histories were placed in the former. This work has resulted in the majority of recent workers considering the Azygiidae to be distinct from the Hemiuroidea, at least at the superfamily level (see Odening, 1974). Work by Powell (1972, 1973, 1975) and Gibson (1974) indicated that it is likely that all cercariae have a syncytial lining to the excretory vesicle. This casts grave doubts upon the validity of La Rue's conceptions.

Yamaguti (1971) stated that life-cycle patterns may be an important systematic feature; but, due to a lack of knowledge with regard to the life-histories of this group, this aspect appears to be of little use in its classification. The little that is known suggests that, even within one family, the life-cycle can vary considerably in detail (see Chabaud & Buttner, 1959; Sinclair *et al.*, 1973; Bray & Gibson, 1977). Stunkard (1973) gave a useful four-page summary of the present knowledge of the hemiuroid life-cycle, and Yamaguti (1975) lists much of this information in more detail. Stunkard introduced his contribution as follows: 'The wide divergence of opinion concerning the systematics and classification of the hemiuroid trematodes is the result, in large measures, of lack of knowledge of their life-cycles and developmental stages. Data are meager, fragmentary, often faulty, and sometimes erroneous.' He summarized his findings thus: 'The miracidia of the hemiuroid, azygiid and didymozoid species are unique and very similar. All are aciliate, provided with an anterior circle of spines, and the surface of the body bears bristles . . . The cercariae develop in rediae; they lack penetration and cystogenous glands, and develop into the cystophorous stage which is characteristic for hemiurid trematodes. Typically they are eaten by copepods and the metacercariae occur as unencysted larvae in the hemocoel of the crustaceans or other planktonic invertebrates that feed on copepods . . . The striking similarity of the larval stages, and the fact that they are peculiar to the hemiurid trematodes, portends genetic homogeneity and despite adult adaptations to different situations, the thesis of Odhner and Führmann that the Azygiidae, Hemiuridae and Didymozoidae are closely related is probably correct'. We agree that these groups do seem to be closely related, although we are reluctant to place too much emphasis on larval stages, especially considering the recent work of Devaraj (1972) and Schell (1975), who have described ciliated, non-spinous miracidia for the hemiuroids *Isoparorchis hypselobagri* (Billet, 1898) and *Lecithaster salmonis* Yamaguti, 1934, respectively. Similarly, a small number of cystophorus cercaria such as, *Cercaria vaullegeardi* Pelseneer, 1906, are known to develop in daughter-sporocysts and not rediae (see Popiel, 1976). We are not convinced of the primitive nature of the cercaria relative to the adult, because of the morphological similarities between what we consider to be primitive hemiuroids and the aspidogastreans (see below). The hypothesis that the present adult digenean evolved from a mature, free-swimming cercaria-like adult is presented by Cable (1965, 1974). It appears more likely to us that the adult forms from vertebrates arose directly from primitive molluscan parasites, in much the same way as many aspidogastreans, and that the crustacean host and the cercarial stage are more recent developments. Pearson (1972) and Rohde (1972) discuss the two contrasting hypotheses concerning the evolutionary significance of the digenean life-cycle. It seems likely that the morphological differences in cercariae, hitherto used as systematic indicators, are, at least to some extent, the result of the ecological requirements of the life-history. If, for example, the crustacean host is benthic, then the cercarial tail will tend to be of a different shape to that of a species which has a pelagic crustacean host. In other superfamilies, such as the Allocreadioidea, there appear to be major differences in the cercariae of different families. A similar argument also applies when considering the chaetotaxy of cercariae as a systematic criterion. In the latter case there is no reason why the hypertrophy or atrophy of the nervous system does not depend upon the ecological requirements of the life-history. One additional disadvantage in using larval characteristics or life-history for systematic purposes, is that for the majority of determinations only adult-specimens are available for study. The lack of knowledge with regard to the larval stages and life-histories of the great majority of genera, however, remains the greatest limitation to their value in systematics. We suggest, therefore, that the use of life-history details, and particularly cercarial morphology, should be treated with *at least* as much caution as the use of adult morphology.

We consider that neither the gross morphology of the adult, due to its variability, nor the use of life-cycle patterns and cercarial morphology, due to a lack of knowledge and understanding with regard to their significance, are able to provide us with a satisfactory classification. In our opinion, functional morphology appears to offer the best alternative. In order to use this concept, one must have a detailed knowledge of the morphology of an organ or organ-system and an understanding of its probable function. Once its function is understood, one can then comprehend the requirements for such an organ in order that the animal might complete its life-history. With an understanding of the function and requirement for particular organs and organ-systems, one can rationalize many of the diverse variations which occur in different taxa, and recognize where development or atrophy has occurred. This sheds light, not only upon the systematics, but also upon the phylogenetic relationships of the taxa. It also tends to expose inaccurate descriptions and is a useful aid in suggesting the probable structure of particular organs in inadequately described taxa. The following classification, which we propose for the Hemiuroidea, is based, therefore, upon adult morphology associated with an attempted understanding of the function of organs and organ-systems. This functional aspect has permitted us to try and base our concepts upon a combination of features, rather than upon one critical feature.

II. Definitions of hemiuroid structures* with comments on their systematic value and possible function

Accessory excretory organ (*vesicle*) – see *Manter's organ.*

Annulations or *annular plications* – see *plications.*

Blind seminal receptacle – a type of seminal receptacle which does not communicate with the exterior via Laurer's canal, but which is linked to the oviduct by a short duct (Fig. 1) and usually has a thick wall. It serves as a seminal store, and its presence, except in the cases in the Trifoliovariinae and Derogeninae where it appears to have arisen from a canalicular seminal receptacle by the loss of Laurer's canal, appears to be a good systematic feature at the subfamily level. It is worth noting that when a blind seminal receptacle is present, the uterine seminal receptacle (q.v.) is lost. See *seminal receptacle.*

Canalicular seminal receptacle – a large proximal dilation of Laurer's canal which is normally filled with fresh, as opposed to spent, spermatozoa (Fig. 1). This type of seminal receptacle (q.v.) in the majority of cases is possibly a recent adaptation associated with the use of Laurer's canal as a vagina (Gibson & Bray, 1975). See *seminal receptacle.*

Cirrus – an intromittent copulatory organ which is formed from or encloses the male duct only. It is rare in hemiuroids, occurring only in the members of the Hirudinellidae. Although its presence in certain other hemiuroid groups has been indicated in the literature, in two such cases, the hemiurid *Glomericirrus* and the derogenid *Arnola*, our observations of sectioned material show that this structure is definitely absent, there being a sinus-organ (q.v.) present. The occurrence of a cirrus in the Hemiuroidea, therefore, is most likely a feature of importance at the family level. It is unlikely, however, that the 'cirrus' of the hirudinellids is homologous with the cirrus common in many groups of Digenea.

Cirrus sac – a muscular sac which surrounds the terminal portion of the male duct including the cirrus. Its function appears to aid the eversion of the cirrus (q.v.) and the expulsion of spermatozoa, as it often encloses the seminal vesicle (q.v.), during copulation by exerting hydrostatic pressure upon its contents. It is to some extent, therefore, analogous with the sinus-sac (q.v.). This structure occurs in the Hirudinellidae: its reported presence in other hemiuroid groups, such as the Halipeginae, we consider to be extremely doubtful. The presence of a cirrus-sac is in our opinion a feature of importance at the family level in the Hemiuroidea.

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* It should be noted that a smaller glossary of terms used in hemiuroid systematics was produced by Manter (1970). There are, however, significant differences between some of our definitions and those of Manter.

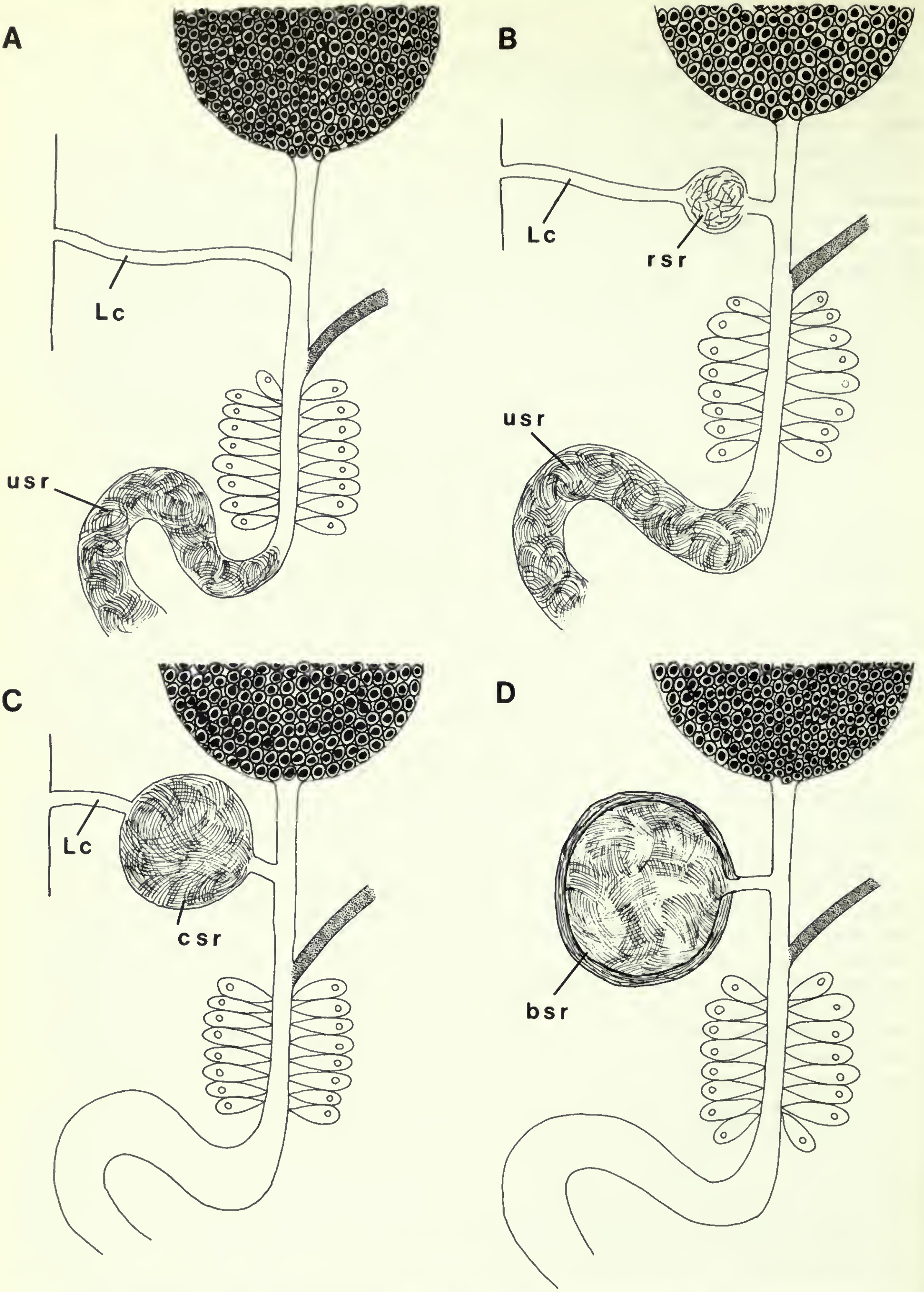

Fig. 1. The different types of seminal receptacle present in the Hemiuroidea: A. Uterine seminal receptacle; B. Rudimentary seminal receptacle; C. Canalicular seminal receptacle; D. Blind seminal receptacle. [bsr, blind seminal receptacle; csr, canalicular seminal receptacle; Lc, Laurer's canal; rsr, rudimentary seminal receptacle; usr, uterine seminal receptacle.]

Cyclocoel – the name given to the gut-caeca when fused terminally, thus forming a complete caecal ring. The advantage of this caecal arrangement is unknown. This feature is of generic importance only, as it occurs widely in unrelated groups both within and outside the Hemiuroidea. The apparent cyclocoel found in large specimens of *Hirudinella* appears to be a subterminal fusion of the gut-caeca which takes place during the development of the animal.

'*Drüsenmagen*' – this structure, the name of which means 'glandular stomach', is found at the 'shoulder'-region of the gut-caeca in many hemiuroids. It is usually an expanded region lined by large, glandular cells forming a villous luminal surface, which is readily distinguished from the lining of the remainder of the caecum. Its function is not known, but it is probably a region of specialized secretion and/or digestion. It does not appear to be of systematic significance as it occurs widely in distantly related hemiuroids, but it is apparently absent in the azygiids. Manter (1970) refers to these structures as 'precaecal sacs'.

Ecsoma – this is the name given to the posterior region of the body of an adult digenean, when it is capable of being retracted within the body (soma). This structure, which appears to be unique to the Hemiuridae, is occasionally referred to as a 'tail' or the specimens are referred to as 'appendiculate' or 'ecsomate'. The gut-caeca, uterus and, on rare occasions, the ovary and vitellarium may extend into the ecsoma, and the excretory pore opens terminally on it. The mechanism of extension is not known, although the body-wall clearly contains longitudinal and circular muscles; but within the ecsoma are numerous large, vesicular cells which might be involved with this process, acting as a hydrostatic skeleton. Its function is thought to be that of a feeding organ which is extruded during periods when the pH or the osmolarity of the stomach contents is at a tolerable level. It should be noted that hemiurids tend to occur in the lumen of the stomach, especially the pyloric region, of marine teleosts and are, therefore, subject to great variations in pH and osmolarity (MacKenzie & Gibson, 1970). We suggest that other groups present in the stomach of these fish, such as the derogenines, tend to live more in the cardiac end of the stomach and only migrate down into the lumen during periods of more neutral pH and/or low osmolarity. These suggestions are made on the basis of observations of *Derogenes varicus* and *Hemiurus communis*. In relation to this function, the development of the ecsoma appears to be associated with the development of plications (q.v.) of the tegument.

As the ecsoma occurs only in the hemiurids, this feature is of importance at the family level. In some groups, however, such as in some of the lecithochiriine genera, the ecsoma may be reduced in size.

Egg-filaments – in a few hemiuroids the egg-shell may be drawn out at the poles to form filaments. Usually, these are unipolar and may be of variable length. Occasionally, they are bipolar and may bear more than one filament (e.g. *Anguillotrema*). It is likely that these filaments are part of a mechanism associated with the acquisition of the first intermediate host. They may, for example, become attached to the gill-filaments of the mollusc. In the case of *Hypohepaticola*, which tends to be a tissue-parasite, the spine-like filament may aid the exit of the egg from the tissue by a mechanism similar to that found in schistosomes. The presence of egg-filaments is a feature of only generic importance, as it occurs spasmodically throughout the group, particularly in the Derogenidae.

Ejaculatory duct – the entire male duct distal to the seminal vesicle can theoretically be referred to as the ejaculatory duct. Regions such as the pars prostatica (q.v.) and cirrus (q.v.) are modifications of the ejaculatory duct. In the hemiuroids, however, the region generally referred to as the ejaculatory duct is an unmodified region of this duct and is, therefore, without an alternative name. When present, it occurs between the pars prostatica and the hermaphroditic duct (q.v.) [or terminus of the male system]. It may occur entirely or partly inside or outside the sinus-sac (q.v.). This region of the duct is of little systematic importance, except perhaps at the specific level; but it is long in certain lecithasterids, especially in the Macradenininae. Occasionally, unmodified regions of the male duct occur between the seminal vesicle and the pars prostatica or separating two regions of the pars prostatica. These regions, however, are not referred to as the ejaculatory duct, but usually as tubular extensions of the seminal vesicle or aglandular regions of the pars prostatica.

Ejaculatory vesicle – a dilation of the ejaculatory duct (q.v.) within the sinus-sac (q.v.). This feature occurs in certain lecithochiriine genera and, in its glandular form (see *prostatic vesicle*), in the Glomericirrinae, Hysterolecithinae and the remainder of the lecithochiriines. It appears to function as a small seminal reservoir as part of a mechanism to increase the amount of spermatozoa ejected from the sinus-sac during copulation. Nasir & Diaz (1971) suggest that an ejaculatory vesicle is merely a prostatic vesicle from which the cellular lining has been lost, hence we suggest that it might be more appropriate to refer to the prostatic vesicle as a 'glandular ejaculatory vesicle' (see p. 93). The presence of an ejaculatory vesicle or a glandular ejaculatory vesicle (prostatic vesicle) is a feature of importance at the subfamily level.

Excretory vesicle (*bladder*) – in hemiuroids this is essentially Y-shaped, the arms often uniting dorsally to the pharynx or oral sucker. The presence of blind arms is a feature of no more than generic importance, as it appears to occur widely in distantly related forms, and indeed we have not used it at the generic level in the case of the azygiid genus *Otodistomum*. There are a number of modifications of the basic structure of this organ, especially in the stouter hemiuroids. These include: (1) in the Sclerodistomidae there are one or two Manter's organs (q.v.), often called 'accessory excretory vesicles', which communicate with this organ distally; (2) in *Hirudinella*, *Botulus* and *Sclerodistomum* the arms form a branching system of tubules or diverticula; (3) in some of the primitive groups, such as the Accacoeliidae, Hirudinellidae and Syncoeliidae, the excretory arms are usually arranged so that initially they pass forward dorsally and ventrally, instead of laterally; and (4) in the Ptychogonimidae the excretory arms unite twice in the forebody.

Fischthal's organ – this is a name given by Yamaguti (1971) for a round vesicle of unknown function, lined with epithelial cells and surrounded by a dense mass of gland-cells, which apparently opens dorsally to the right of Mehlis' gland (q.v.) in *Pelorohelmins palawanensis* Fischthal & Kuntz, 1964. There is no evidence of such a structure in specimens under the name of *P. ghanensis* Fischthal & Thomas, 1968, from the collection of the British Museum (Natural History). It is possible, therefore, that Yamaguti may have mistaken Juel's organ (q.v.) for this structure. He also, however, describes this structure in *Meristocotyle varani* Fischthal & Kuntz, 1964, a species of unknown relationship; but in this case it is the distal dilation of Laurer's canal which opens dorsally. [We should point out that we regard *Pelorohelmins* to be a synonym of *Elongoparorchis*.]

Genital atrium – a receptacle present in most hemiuroids between the hermaphroditic duct and the genital pore, which probably acts as a vagina during copulation. Spermatozoa are probably deposited within this structure by the copulatory organ of another worm when cross-insemination occurs, and it is then either sucked back into the hermaphroditic duct by the action of the sinus-sac or, more likely, forced back (the sinus-organ being retracted to receive it) by the action of the muscular walls of the genital atrium which are contractile. The lining of the genital atrium is continuous with the sinus-organ (or in the case of the hirudinellids, the 'cirrus'), and appears to contribute significantly to the formation of its outer surface as it extends. In some of the hirudinellids the genital atrium may be everted through the genital pore, thus giving extra length to the 'cirrus' (see Fig. 12D of Gibson & Bray, 1977). This also occurs in *Isoparorchis* (Fig. 2), where it adds additional length to the sinus-organ.

The contractile nature of this organ makes it of limited taxonomic value, even at the specific level, although its apparent total absence may be of some value. It is often reduced or absent in species which must rely upon self-insemination or which possess only a temporary sinus-organ. When the sinus-organ and sinus-sac are absent, it is difficult to distinguish the genital atrium from the hermaphroditic duct. In such cases, these two terms often appear to have been used interchangeably.

Genital pore – the aperture through which the contents of the genital ducts pass to the exterior. It usually, in the Hemiuroidea, forms the mouth of the genital atrium, but occasionally occurs at the distal end of the hermaphroditic duct, when the genital atrium (q.v.) is absent, or at the union of the male and female ducts when both the hermaphroditic duct and the genital atrium are absent. The genital pore is not always the most distal part of the terminal genital apparatus, as during copulation the copulatory organ, or even the genital atrium, is thrust through the genital

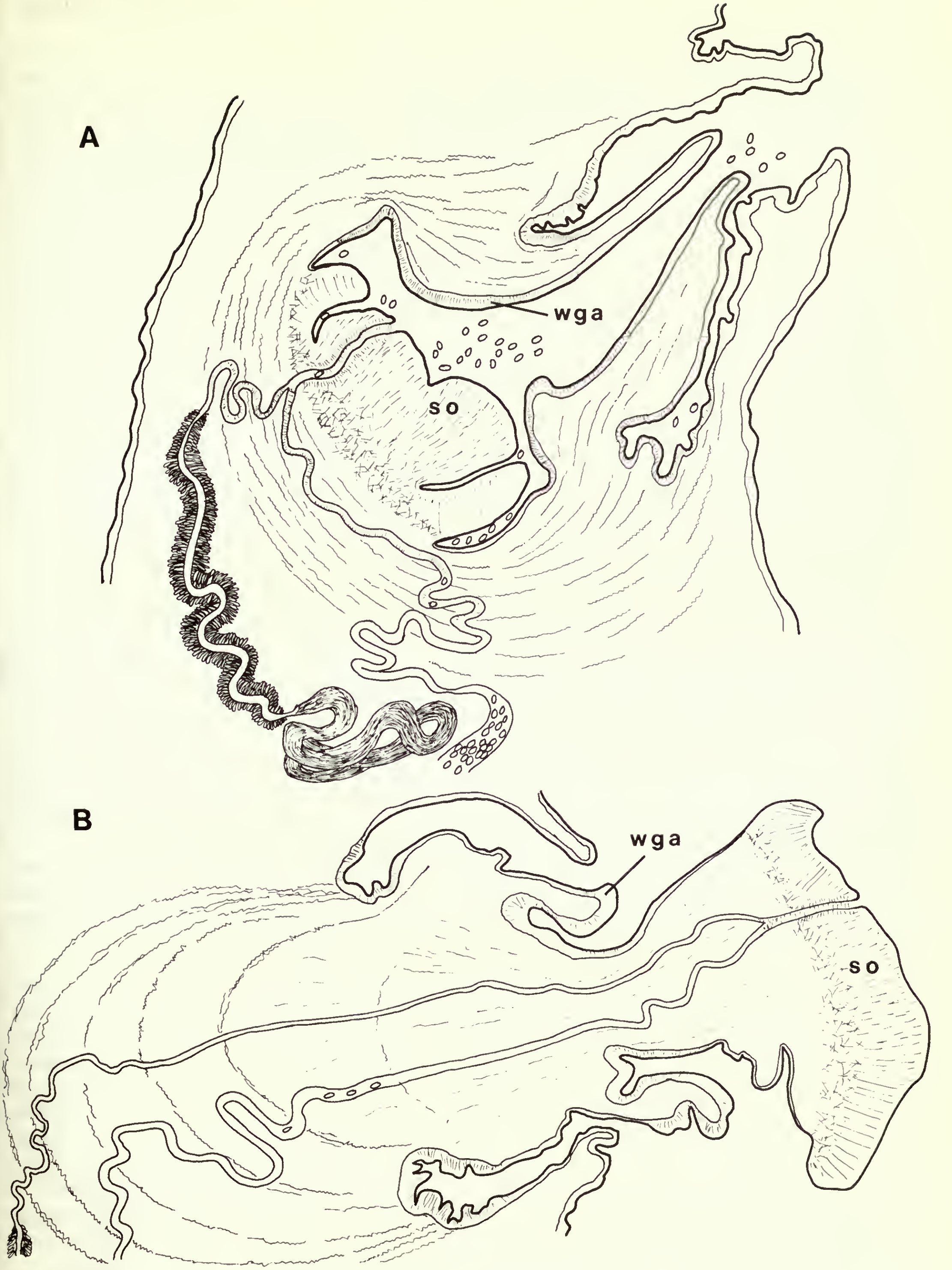

Fig. 2 Sagittal sections through the terminal genitalia of *Isoparorchis*: A. Withdrawn; B. Extruded. [so, sinus-organ; wga, wall of genital atrium.]

pore. This structure is of little systematic importance as it occurs mid-ventrally in the anterior forebody in all hemiuroids.

Hermaphroditic duct – a duct commonly linking the terminal male and female ducts with the genital atrium. The duct itself appears to have arisen partly as a modification of the genital atrium and partly from the fusion of the male and female ducts. It is normally quite distinct from the genital atrium; but, in certain cases, when the sinus-sac and sinus-organ are absent, it is difficult to distinguish these structures. An hermaphroditic duct occurs in most hemiuroids, commonly within the sinus-sac and almost always within the sinus-organ, when the latter structure is present. Annular muscles are sometimes clearly seen in its walls, e.g. *Elytrophalloides*, and probably serve to transport eggs and spermatozoa along its length by peristalsis. In some genera, such as *Paradinurus* and *Hemiurus*, the proximal part of the hermaphroditic duct is lined by villous, glandular cells of unknown function: this region may serve a similar function to the prostatic vesicle (q.v.) of the lecithochiriines. The distal part of the hermaphroditic duct in *Hemiurus* is lined with cuticular papillate structures: as this is the region which forms the outer surface of the temporary sinus-organ, it presumably aids the maintenance of the union during copulation. There are indications in *Halipegus* that the hermaphroditic duct in some species of this genus may be transitory, developing from the sinus-organ as it extends.

The absence of an hermaphroditic duct, except in the case of the Hirudinellidae and in *Halipegus*, is of generic importance only, because of: (1) the inability to distinguish it in some cases from the genital atrium; and (2) the fact that degeneration of the terminal genitalia, due to the increasing importance of self-insemination, appears to have occurred independently on a number of occasions.

Hermaphroditic sac – see *sinus sac.*

Inner vesicle – this is the name given by Juel (1889) to the sac-like structure (Fig. 3), filled with active and/or disintegrating spermatozoa found within the structure which we have called Juel's organ (q.v.). In the rudimentary form of Juel's organ (see *rudimentary Juel's organ*) this sac-like structure has not been enveloped, and is referred to here as a 'rudimentary seminal receptacle' (q.v.). According to Juel (1889) and Lander (1904), the inner vesicle normally appears to have an aperture at its distal end, and presumably it is through this that the disintegrating spermatozoa and vitelline material pass into the outer, amorphous mass of Juel's organ. The inner vesicle, which may be oval or in the form of a convoluted tube, appears to act, therefore, as a 'killing chamber' for the excess reproductive material.

This structure is present in all of the groups where a fully developed Juel's organ occurs, and its taxonomic significance is as discussed for the latter organ. It should be noted that in the case of certain didymozooids the inner vesicle does not appear to be entirely enveloped by the outer mass of Juel's organ.

Juel's organ – in many hemiuroids, and all hemiurids, Laurer's canal does not open dorsally, but leads into an organ which has been referred to as a 'seminal receptacle' or, more recently 'the pouch of Laurer's canal' (Madhavi & Rao, 1974). It was apparently first described by Juel (1889), and we, therefore, felt (Gibson & Bray, 1975) that Juel's organ was an appropriate designation. It consists of an oval or globular sac containing an amorphous granular material, with the occasional (?) amoeboid cells embedded in it (Figs 3A & 4A). An 'inner vesicle' (q.v.), either globular and/or tubular, lies within this mass and contains spent (but often active) or partly disintegrated spermatozoa, vitelline material and, occasionally, ova. The inner vesicle is fed by Laurer's canal, which may be long or short, depending upon the proximity of Juel's organ to Mehlis' gland. The other end of the inner vesicle opens into the outer mass of Juel's organ. Sometimes Juel's organ and Mehlis' gland are apparently enclosed by a common membranous sheath, but in other species Juel's organ lies outside the sheath surrounding Mehlis' gland.

The function of Juel's organ is, apparently, as a disposal unit for excess reproductive material, which enables these resources to be recycled and is thus economically advantageous to the worm compared with the situation where Laurer's canal acts as a drain for these products. It is possible

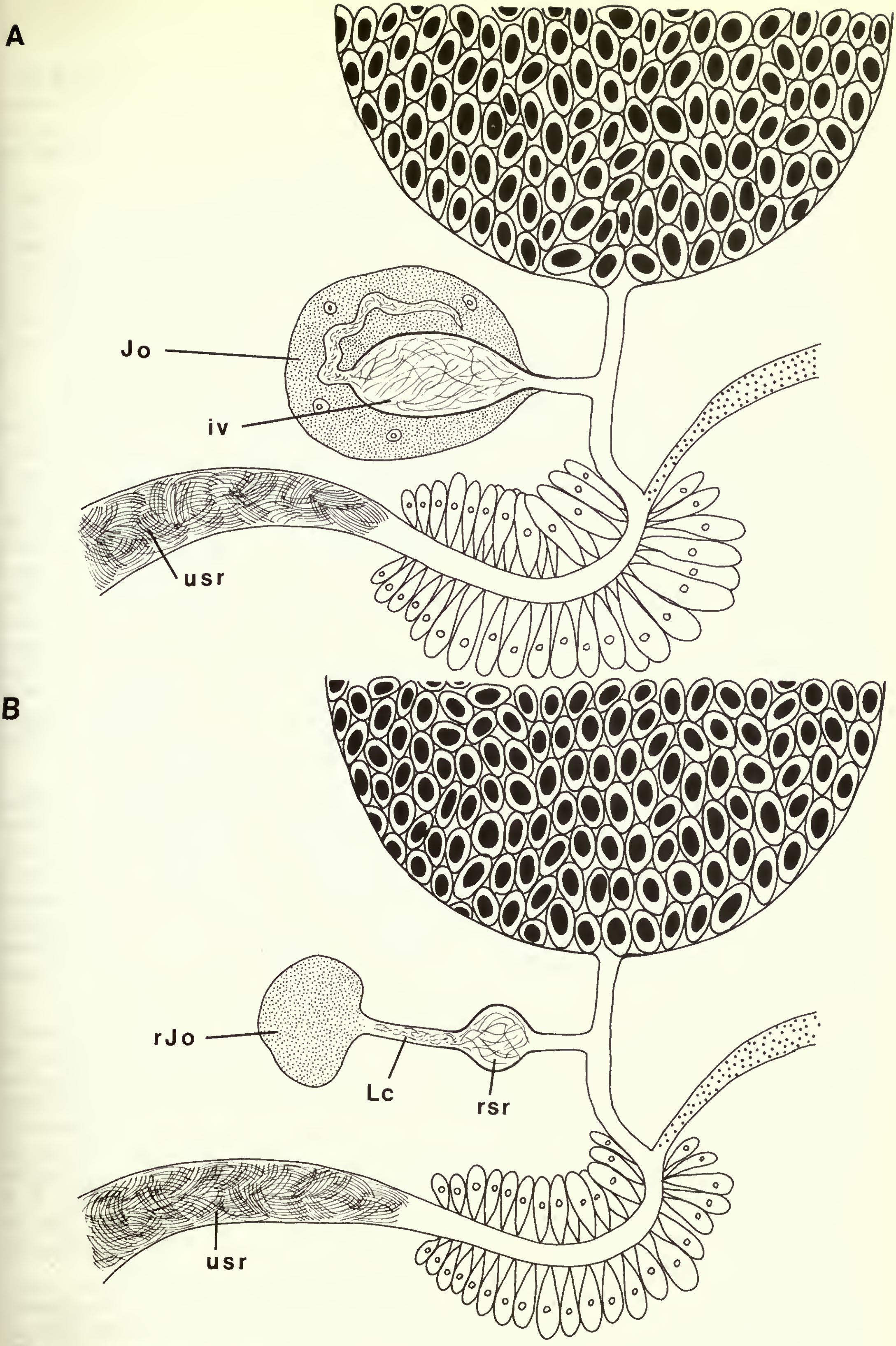

Fig. 3 Diagrammatic representation of a fully developed (A) and a rudimentary (B) Juel's organ. [iv, 'inner vesicle'; Jo, Juel's organ; Lc, Laurer's canal; rJo, rudimentary Juel's organ; rsr, rudimentary seminal receptacle; usr, uterine seminal receptacle.]

that the (?) amoeboid cells in the outer mass of Juel's organ might be involved in the final breakdown of this waste material. A fully developed Juel's organ is found in all hemiurids (*sensu stricto*), the aphanurine bunocotylids, the dictysarcids, the hysterolecithine lecithasterids and in some halipegine derogenid genera. It also occurs, in a slightly modified form, in the nematobothriine didymozooids.

In certain derogenine and sclerodistomid genera Juel's organ possesses no inner vesicle. This form, which we consider to be more primitive, we have referred to as a 'rudimentary Juel's organ' (q.v.). In this case there is usually a rudimentary seminal receptacle (q.v.), from which the 'inner vesicle' is later formed, that leads via a region of Laurer's canal of varying length into an amorphous mass, resembling the outer region of the fully developed Juel's organ (Figs 3B & 4B). The presence of a fully developed Juel's organ we consider to be a feature of significance at the subfamily level, except in the case of the Halipeginae, where it is of generic importance only (but see *Genarchopsis*).

Laurer's canal – a duct which links the oviduct with either the exterior, a seminal receptacle (q.v.) or with Juel's organ (q.v.). Its function has long been a matter of contention. Looss (1893) wrote a paper entitled, 'Ist der Laurers'che Kanal der Trematoden eine Vagina?' and he, Goto (1893) and Johnston (1912) believed that it functioned as a 'sperm-drain'. Cohn (1902, 1903) and Palombi (1931), however, have described examples where Laurer's canal is used as a vagina. This work led Hyman (1951) to state, 'Laurer's canal in flukes was formerly considered to serve as an exit for superfluous sperm and yolk cells but is now known to function in copulation'. Our recent work (Gibson & Bray, 1975) with hemiuroids has indicated that Laurer's canal does in fact function in this group as a drain for excess and/or spent seminal and vitelline material, and we suggest that in other groups the use of this canal as a vagina during copulation is a more recent development associated with the loss of a uterine seminal receptacle (q.v.) and the development of a functional seminal receptacle as a proximal dilation of this canal, i.e. a canalicular seminal receptacle (q.v.). It should be noted that Juel's organ appears to be a modification of Laurer's canal. The nature of Laurer's canal and its presence or absence are often useful features at the subfamily or family level, except in the cases of the Derogeninae, Halipeginae, Prosorchiinae and Trifoliovariinae.

Manter's organ (*accessory excretory organ* or *vesicle*) – a tubular vesicle lined with an epithelium and usually surrounded by bundles of muscle, especially longitudinal muscle. It occurs dorsal to the excretory vesicle (q.v.) into which it opens postero-ventrally close to the excretory pore. It is a feature of the Scerodistomidae, occurring singly in *Prosogonotrema*, *Prosorchis* and *Prosorchiopsis* and paired in *Sclerodistomum*. Gibson & Bray (1977) suggest that it might occur in *Distoma gigas* Nardo, 1827, a giant digenean of uncertain systematic position. The name Manter's organ appears to have been coined by Yamaguti (1971), and is in our opinion more acceptable than the appellation 'accessory excretory organ (vesicle)', as the function of this organ is unknown.

Mehlis' gland – a cluster of gland-cells which surround the region of the ovovitelline canal which links the oviduct and the uterus: this is usually the region of the oötype (q.v.). It is thought to produce a mucous secretion which lubricates the uterus and a lipoprotein secretion which forms a membrane around the ovum and vitelline cells upon which shell-material is then deposited (Smyth, 1966). It also seems likely that it may produce a secretion which activates the spermatozoa.

Mehlis' gland appears to be of little systematic importance, except that, although in the majority of hemiuroids it is post-ovarian [the oviduct leaves the ovary posteriorly], in the azygiids and accacoeliine accacoeliids it is pre-ovarian [the oviduct leaves the ovary anteriorly]. It is likely that there are several exceptions to this rule, such as the prosorchiine sclerodistomids. In certain hemiuroids Mehlis' gland appears to be enclosed along with Juel's organ by a membranous sac (see Madhavi & Rao, 1974).

Metraterm – a name given to the terminal region of the uterus, when it can be distinguished morphologically from the rest of this organ. It is of little taxonomic importance in this group, as it is usually difficult to distinguish and often tends to grade into the uterus-proper. It is usually

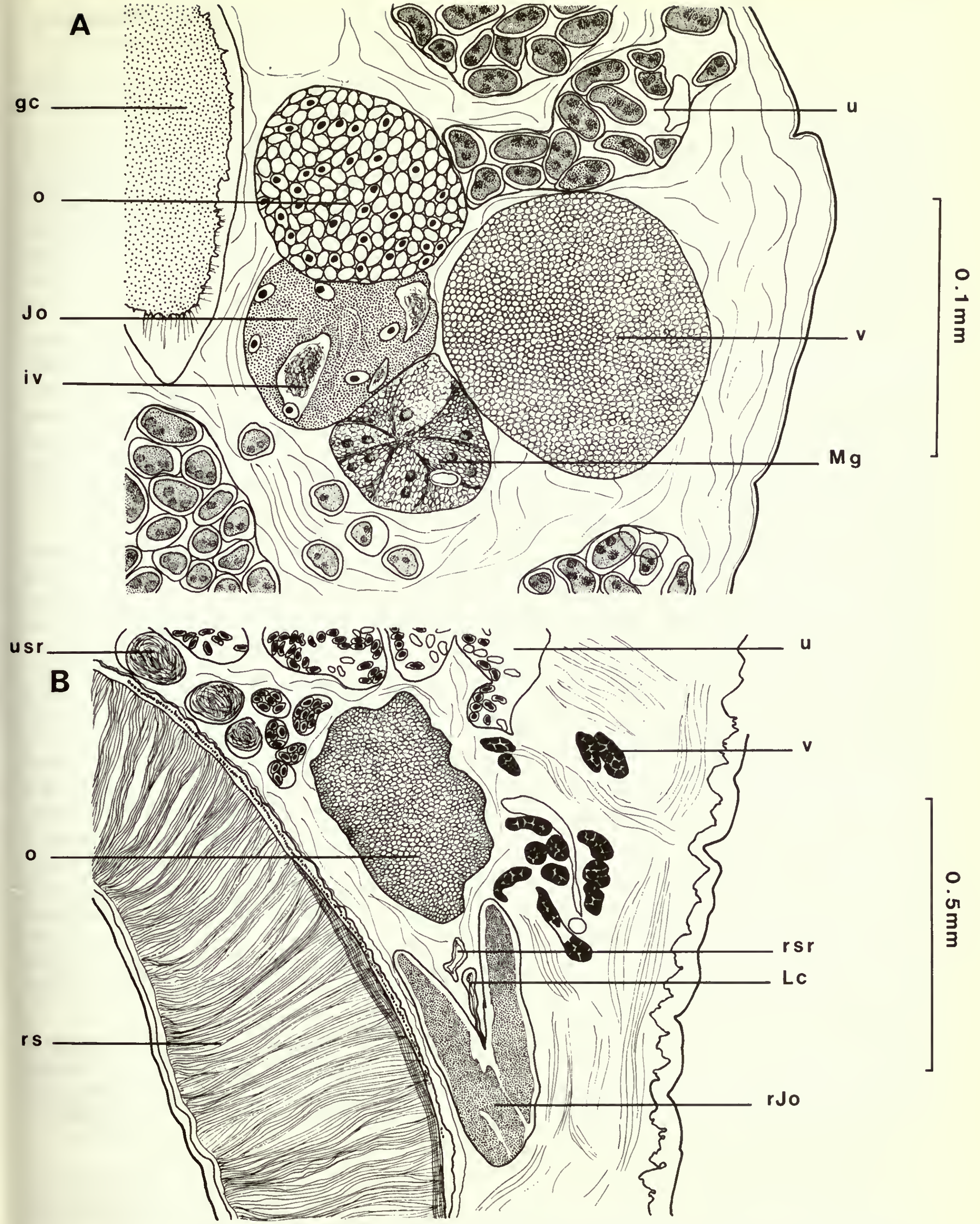
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Fig. 4 Sections of a fully developed (A) and a rudimentary (B) Juel's organ. [gc, gut-caeca; iv, inner vesicle; Jo, Juel's organ; Lc, Laurer's canal; Mg, Mehlis' gland; o, ovary; rJo, rudimentary Juel's organ; rs, ventral sucker; rsr, rudimentary seminal receptacle; u, uterus; usr, uterine seminal receptacle; v, vitellarium].

muscular, often surrounded by small gland-cells and in some dinurines it has a villous lining. In *Erilepturus* (=*Uterovesiculurus*) it appears to form a distinct dilate sac.

Oötype – a region of the female duct (ovovitelline canal) where egg-formation and possibly fertilization occur. This is normally the region, surrounded by Mehlis' gland (q.v.), which links the oviduct with the uterus. In the hemiuroids this region does not appear to be vesicular as in many other digeneans, but is present as a narrow tube. Although we have seen soft egg-shells in this region in *Isoparorchis*, *Otodistomum* and some hemiurids, in others, such as *Derogenes*, *Pulmovermis* and *Syncoelium*, the oötype appears to extend into the first part of the uterus, as egg-shell formation occurs in a region not surrounded by Mehlis' gland. We are referring to this region as a *uterine oötype* (q.v.). The systematic significance of these variations of the oötype have not been studied; but it seems unlikely that they may be of any value above, perhaps, the generic level.

Ovary – in the hemiuroids this is usually oval in shape, but in certain groups, such as the lecithasterids, syncoeliids and dictysarcids, it is commonly composed of 4 or 5 distinct lobes. In one instance (*Isoparorchis*) the ovary is tubular. The position of the ovary in relation to the testes is an important systematic criterion at the subfamily level, except in the case of some of the macrodeninine lecithasterids. The ovary is post-testicular in most groups, but is pre-testicular in the azygiine azygiids, the ptychogonimids, the gonocercine derogenids and certain macradeninine lecithasterid genera, and occurs between the testes in the bathycotylids. The ovary occurs in the hindbody in all groups, except for the prosogonotrematine sclerodistomids.

Oviduct – the duct linking the ovary and the oötype (q.v.). It receives Laurer's canal and the common vitelline duct before, or sometimes in the case of the common vitelline duct, slightly after entering Mehlis' gland (q.v.). The oviduct appears to leave the ovary posteriorly in the majority of hemiuroids, the exceptions being the azygiids, the accacoeliine accacoeliids and possibly odd genera, such as *Prosorchiopsis*, in other groups.

Pars prostatica – the region of the male duct between the seminal vesicle and either the ejaculatory duct or the hermaphroditic duct. It is normally surrounded by prostatic gland-cells and lined by what appear to be anuclear gland-cells which often project into the lumen presenting a papillate or villous appearance: it is possible, however, that the latter are merely internal extensions of the outer gland-cells. The function of this region is not known for certain, but it may produce a secretion which protects and lubricates the spermatozoa during ejaculation. It may also be involved in the activation of spermatozoa during ejaculation. The shape of this duct, i.e. whether it is vesicular or tubular, is of specific value, and so is its length. The presence of a vesicular pars prostatica has often been confused with a prostatic vesicle (q.v.). When the external gland-cells are severely restricted in their distribution by surrounding parenchyma or are bound by a fibrous membrane, they are spoken of as being 'delimited'. In certain cases an aglandular duct links the pars prostatica and the seminal vesicle; this is usually referred to as a tubular extension of the seminal vesicle or as an aglandular region of the pars prostatica. An aglandular region also links the two parts of the pars prostatica in the dinurine hemiurid *Mecoderus*.

Peduncle – this is a stalk upon which the ventral sucker may be surmounted. It occurs only in a few species of hemiuroids. It may be of some taxonomic importance at the generic level; but it is often variable in size, sometimes being either difficult to distinguish or prominent in the same species, e.g. in *Accacladium serpentulum* Odhner, 1928, as described by Bray & Gibson (1977).

Permanent sinus-organ – see *sinus-organ* (*permanent*).

Plications – regular backwardly directed thickenings of the tegument which surround or partly surround the body transversely. They are a feature unique to the hemiurids and the aphanurine bunocotylids; but only occur in certain genera, being a feature normally considered to be of systematic importance at the generic level (a notable exception being the genus *Aphanurus*, but see p. 65). They may occur over the whole body (soma) or just part of it, and tend to be better developed anteriorly than posteriorly, especially in the dorsal field. They are never present on the ecsoma. Care should be taken not to confuse these regular tegumental thickenings with a rugate appearance caused by contraction, with small transverse ridges caused by circular muscles in the body-wall of poorly preserved material (these do occur on the ecsoma), and with transverse folds of the body-wall surrounding the suckers of certain bunocotylid genera.

Plications appear to be a primitive hemiurid feature which arose in association with the ecsoma (q.v.). They are possibly a feature which permits the thickening of the somatic tegument during periods of low pH or high osmolarity when the ecsoma is withdrawn, and yet still allows full and easy extension and contraction of the body during periods of activity. Certain genera, which possibly no longer inhabit the pyloric region of the stomach or which are parasitic in physiologically 'stomachless' fish (see Barrington, 1957), have lost this feature.

Pre-acetabular pit – see *presomatic pit.*

Precaecal sac – see '*Drüsenmagen*'.

Pre-oral lobe – a small region of the body anterior to the oral sucker. In some instances it may actually overhang the anterior margin of the oral sucker. It has no apparent systematic importance, except that it is glandular in one species of *Otodistomum* (see Gibson & Bray, 1977), as it appears to occur, at least to some extent, in all hemiuroids.

Presomatic pit (*preacetabular pit*) – a deep, concave depression, circular or oval in section, which is present mid-ventrally just anterior to the ventral sucker. It occurs in certain lecithochiriine genera, in the plerurine genus *Synaptobothrium* and apparently in the aphanurine genus *Mitrostoma.* Great care should be taken in its use as a taxonomic criterion as it is easily confused with the ventro-cervical groove (q.v.), which is common in many hemiurids. In the genus *Lecithochirium* this structure can be either present or absent, being very small and difficult to distinguish in the type-species: this does not appear, therefore, to be a useful character in distinguishing *Lecithochirium* and *Sterrhurus* (see p. 93).

The presomatic pit often has a region of glandular tissue around its base; but its actual function is not understood. Lloyd (1938) has suggested that it acts as a chemo-sensory organ and that it may be associated with the extrusion and withdrawal of the ecsoma: it would appear that the latter certainly cannot be the case in *Mitrostoma.*

Prostatic sac – a term coined by Gibson (1976) for the muscular sac which surrounds the pars prostatica and the seminal vesicle of the azygiids. Its function is not known for certain, but presumably it aids the evacuation of spermatozoa and prostatic secretion during ejaculation.

Prostatic vesicle – a dilation of the ejaculatory duct within the sinus-sac, which is usually lined by glandular cells and occurs in addition to an external pars prostatica. Essentially, it is identical to an ejaculatory vesicle (q.v.), except for the presence of the glandular cells. As the latter cells can apparently be lost, it does seem unwise to distinguish a prostatic vesicle from an ejaculatory vesicle, and, in view of the possibility of confusing the former structure, both nomenclaturally and morphologically, with a 'vesicular pars prostatica' (q.v.), it might be advisable to refer to the prostatic vesicle as being a 'glandular ejaculatory vesicle'. This structure occurs for certain only in the lecithochiriine, glomericirrine and hypohepaticoline genera, and is possibly a feature of importance at the subfamily level (if included as a type of ejaculatory vesicle). We do not consider that this structure occurs in any of the plerurine or pulmovermine genera, for in these cases the pars prostatica itself appears to be partly enclosed by the sinus-sac in cases when the latter is present. The function of a prostatic vesicle is probably identical to that suggested for an ejaculatory vesicle.

Receptaculum seminis – see *seminal receptacle.*

Receptaculum seminis uterinum – see *uterine seminal receptacle.*

Rudimentary Juel's organ – a form of Juel's organ (q.v.) which lacks an 'inner vesicle' (q.v.). It has a granular appearance and is present usually at the distal end (Figs 3B & 4B), but occasionally more proximally, of Laurer's canal. It presumably has a similar function to a fully developed Juel's organ, into which it has probably evolved in more advanced forms by enveloping the rudimentary seminal receptacle (q.v.) and forming an 'inner vesicle'. Small, black structures can be seen within the amorphous mass which fills this organ: we wonder whether these might be bacteria which may carry out the final breakdown of the excess seminal and vitelline material, much as we suggest that (?) amoeboid cells might do in a fully developed Juel's organ.

A rudimentary Juel's organ is known to occur in certain derogenine derogenid and prosogonotrematine and prosorchiine sclerodistomid genera, but its taxonomic significance, even at the generic level, is uncertain. This organ also appears to occur in the aspidogastrean *Aspidogaster conchicola* von Baer, 1826 (see p. 123).

Scales – a term used by Manter (1934) to describe the structures on the tegument of *Dinosoma*. We believe that they are probably just regularly crenulate plications (q.v.).

Seminal receptacle – a general term covering several different types of apparatus for the storage of spermatozoa in the female reproductive system. In our opinion the various forms of seminal receptacle should be clearly differentiated in descriptions, as they are important taxonomic criteria. We recognize four different kinds of seminal receptacle present in the Hemiuroidea (Fig. 1): (1) a 'blind seminal receptacle' (q.v.), which is a blind sac, linked to the oviduct by a short tube, occurring in most of the lecithasterid subfamilies, the opisthadenine bunocotylids and the derogenid genus *Leurodera*, and which appears to have evolved from Juel's organ (q.v.) or in some cases from a rudimentary or canalicular seminal receptacle; (2) a 'canalicular seminal receptacle' (q.v.), which is a large proximal dilation of Laurer's canal, and occurs frequently in other groups of digeneans, but apparently within the Hemiuroidea it occurs for certain only in the lecithasterid genus *Trifoliovarium* and in a modified form in the derogenid genus *Progonus*; (3) a 'rudimentary seminal receptacle' (q.v.), which is a small proximal dilation of Laurer's canal that, when present, always occurs together with a uterine seminal receptacle, but this form differs from the others in that it is not a store of fresh, quiescent spermatozoa and in that the small amount of spermatozoa which it does contain are spent, although often still active; and (4) a 'uterine seminal receptacle' (q.v.), which is a store of spermatozoa present in the proximal region of the uterus, and occurs in the majority of hemiuroids. Another type is an 'oviducal seminal receptacle', which is formed as a dilation of the oviduct; but this type does not occur in the Hemiuroidea. With the exception the 'rudimentary' and 'uterine' types, the various forms of seminal receptacle do not normally occur together in the same individual.

Seminal sac – a term used by Manter (1947) for an oval, muscular sac which encloses a convoluted, tubular seminal vesicle in the bunocotylid *Opisthadena dimidia* Linton, 1910. It appears to be a modification of the muscular type of seminal vesicle where the muscular wall is clearly not associated with the membranous lining of the seminal vesicle. It also occurs in some of the other species of *Opisthadena* and in the hemiurid *Elytrophalloides*.

Seminal vesicle – a dilation of the vas deferens (q.v.) which forms a store of spermatozoa which is ready for ejaculation. It is often provided with a muscular wall or with sphincter muscles which constrict it into portions. These modifications, which are often of systematic importance at the generic level, are involved with the evacuation of spermatozoa from the seminal vesicle, through the pars prostatica and into the hermaphroditic duct, often against the hydrostatic pressure produced by the sinus-sac (q.v.). The shape of the seminal vesicle is also often of specific or generic value, as is its position in relation to the ventral sucker. In the more primitive forms it is usually tubular. In the hemiuroids the seminal vesicle is normally free in the parenchyma, but in certain halipegine derogenids it may be partly or completely enclosed within the sinus-sac, in the azygiids it is contained within a prostatic sac (q.v.), and in certain species of *Opisthadena* it forms a 'seminal sac' (q.v.).

Sinus-organ (*permanent*) – a copulatory organ of variable size which is usually formed externally from the wall of the normally well-developed genital atrium and internally from the hermaphroditic duct. This type of sinus-organ is contractile, but is still visible in sections as a small cone when completely retracted. It usually occurs in one of two forms, although intermediate forms are sometimes found (Fig. 5):

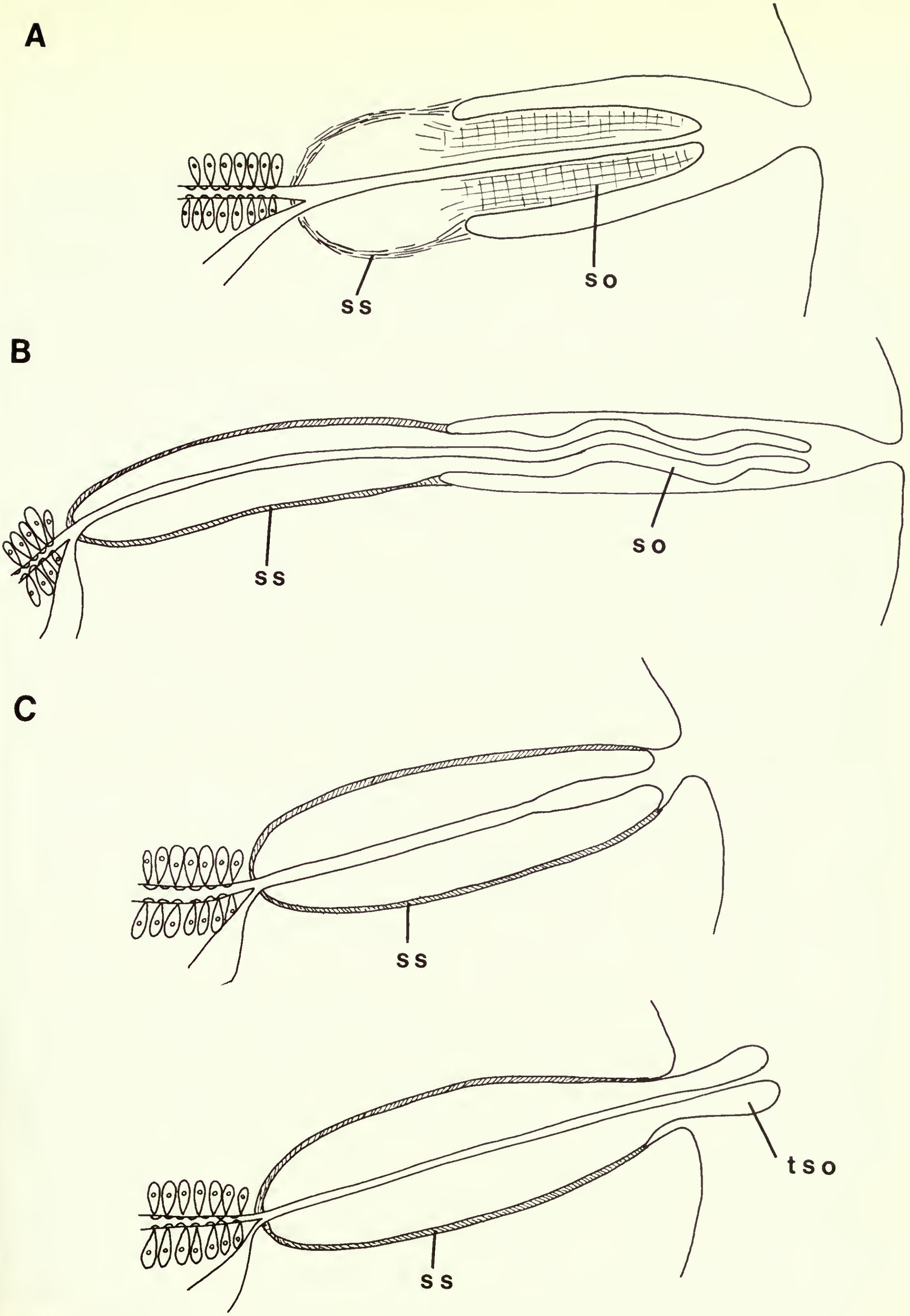
A
so
ss
B
so
ss
C
ss
tso
ss

Fig. 5 The types of sinus-organ occurring in the Hemiuroidea: A. Muscular sinus-organ; B. Amuscular sinus-organ; C. Temporary sinus-organ. [so, permanent sinus-organ; ss, sinus-sac; tso, temporary sinus-organ.]

(1) 'Muscular' – where it is probably everted entirely or partly by its own intrinsic musculature (when partly, the remaining force is supplied by hydrostatic pressure produced by the sinus-sac: see Gibson & Bray, 1974): this form occurs in many of the more primitive hemiuroid groups (see p. 129);

(2) 'Amuscular'* – a form, associated with the presence of a thick-walled (muscular) seminal vesicle, which is probably everted entirely, or almost entirely, by hydrostatic pressure produced by the sinus-sac upon its contents: this form occurs in the elytrophalline and glomericirrine hemiurids, the muscular seminal vesicle being required to force spermatozoa into the hermaphroditic duct against the hydrostatic pressure built up by the walls of the sinus-sac.

The presence or absence and type of sinus-organ are often useful taxonomic criteria up to the subfamily level; but the sectioning of specimens is essential and great caution must be exercised in the use of this feature. See *sinus-organ* (*temporary*).

Sinus-organ (*temporary*) – an amuscular or weakly muscled copulatory organ, formed from the hermaphroditic duct by hydrostatic pressure within the sinus-sac, which is a transitory structure (Fig. 5). It is usually only present during copulation, but also occurs occasionally in fixed specimens. The genital atrium is usually small or apparently absent in forms with a temporary sinus-organ. Naturally 'permanent' [see *sinus-organ* (*permanent*)] and 'temporary' types of sinus-organ cannot occur in the same species of worm. The two forms, however, may be difficult to distinguish when only a small number of specimens is available for study. A temporary sinus-organ may be associated with slight thickenings in the wall of the seminal vesicle, but is more often associated with the presence of sphincter muscles which tend to partition the seminal vesicle and are capable of exerting pressure, thus forcing spermatozoa into the sinus-sac against its internal hydrostatic pressure during ejaculation. As the genital atrium tends to be short or absent, the temporary sinus-organ itself is also short, and, therefore, the hydrostatic pressure required to extrude it is reduced. The sinus-sac tends, therefore, to be smaller than in forms with an amuscular permanent sinus-organ. A temporary sinus-organ occurs in the more advanced forms of hemiurids, bunocotylids and lecithasterids. As this transitory structure is rarely seen everted, it is of no systematic significance.

Sinus-sac or hermaphroditic sac – a muscular sac which surrounds the base of the genital atrium, if present, and encloses the hermaphroditic duct and/or the terminal portions of the ejaculatory duct and uterus. Its apparent function is to aid the eversion of a permanent sinus-organ (q.v.) or the production of a temporary sinus-organ (q.v.) from the hermaphroditic duct. It may also aid the expulsion of spermatozoa and eggs, especially the former in cases where an ejaculatory (or prostatic) vesicle (q.v.) or the seminal vesicle is enclosed within the sinus-sac. In certain instances, e.g. in some of the plerurine hemiurids, there may be a large proximal gap in the wall of the sinus-sac at the point through which the male and female ducts pass: this is known as an 'open-type' of sinus-sac and is probably a vestigial form. In other groups of hemiuroids the sinus-sac may be reduced, or in some cases completely lost. Sectioning is essential when the sinus-sac is apparently absent, as the vestiges of this structure are often insignificant. This feature is frequently of some importance at the family level, as it is missing in the Azygiidae and Hirudinellidae, which possess a 'prostatic sac' (q.v.) and a 'cirrus-sac' (q.v.), respectively; but great care should be exercised in the utilization of this feature, as it appears to have been lost independently in certain genera from a number of distantly related hemiuroid groups, e.g. *Gonocerca*, *Syncoelium*, *Tetrochetus*, *Prolecitha* and *Bunocotyle*.

Temporary sinus-organ – see *sinus-organ* (*temporary*).

Testes – there are usually two globular testes present in hemiuroids. Exceptions are the syncoeliids, which either have a much larger number (11–18) of large oval masses (referred to as testes, although there are only two vasa efferentia) or possess apparently follicular testes, and two lecithasterid genera, *Monorchiaponurus* and *Monorchimacradena*, which are reported to have one testis.

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* Presumably there are some longitudinal muscle fibres present which permit contraction of this type of sinus-organ.

An important feature at the subfamily level (except in some members of the Macradenininae) is the relationship between the ovary and the testes, the ovary usually being post-testicular. In the azygiine azygiids, the ptychogonimids, the gonocercine derogenids and certain macradeninine lecithasterids, however, it is pretesticular, and in the bathycotylids it is inter-testicular. The relative positions of the testes and their shape are of little value above the specific level, except that in the dictysarcid genus *Elongoparorchis* they do appear to be consistently elongate. The testes normally occur in the hindbody, except in the prosogonotrematine and prosorchiine sclerodistomids.

Uroproct – the aperture of the excretory vesicle when the base of the latter organ communicates directly with the distal extremities of the gut-caeca. A uroproct, therefore, serves as an orifice for the evacuation of waste-products from both the excretory and alimentary systems. This structure occurs independently and regularly in the Accacoeliidae, Hirudinellidae, Ptychogonimidae and Otiotrematinae, but, except for the Accacoeliinae and the Ptychogonimidae, it does not occur in all of the genera in these groups. It is normally considered to be a feature of generic importance.

Uterine oötype – the proximal region of the uterus, present in some species, into which the region of egg-formation extends. Its systematic importance is not understood. See *oötype*.

Uterine seminal receptacle or *receptaculum seminis uterinum* – a term given to the proximal region of the uterus when it is filled with 'fresh' spermatozoa and is, therefore, acting as a seminal store (Fig. 1). This region can normally only be differentiated from the remainder of the uterus by the presence of spermatozoa. It is the commonest form of seminal receptacle (q.v.) present in the Hemiuroidea, being absent only in the lecithasterids (with the exception of the Hysterolecithinae), the opisthadenine bunocotylids and in the derogenids *Progonus* and *Leurodera*. This type of seminal receptacle is probably associated with cross-insemination, using the genital atrium as a vagina, or with self-insemination, and differs from all other types of seminal receptacle in that spermatozoa pass towards the ovary through the oötype. In the past many workers have mistaken this structure for a canalicular seminal receptacle (q.v.), but in sectioned material the two can easily be distinguished. Except in the cases of the derogenids *Progonus* and *Leurodera*, the presence or absence of this type of seminal receptacle is an important systematic feature at the subfamily level. Great care must be exercised with the use of this feature because it is by nature transitory, and, when empty, it is not recognizable as a seminal store. We have observed, in sectioned material, specimens of *Hirudinella* and *Prosorchiopsis* (forms possessing a uterine seminal receptacle) which do not have any spermatozoa in the proximal region of the uterus.

Uterus – a duct, normally full of eggs, which links the oötype with the hermaphroditic duct, genital atrium or genital pore. The distal extremity may be modified to a form metraterm (q.v.), and the proximal extremity may form a uterine seminal receptacle (q.v.) or a uterine oötype (q.v.). In addition to transporting eggs, the proximal region of the uterus appears to be involved in the hardening and tanning of the egg-shells. The uterus often coils between the ovary and the ventral sucker, but it may loop well posterior to the ovary and in some cases coils in the forebody. Its distribution tends to be of generic importance and occasionally of subfamilial importance, especially in cases where it reaches into the post-ovarian field or is entirely pre-ovarian.

Vasa efferentia – single narrow ducts which connect each testis with the vas deferens (q.v.). In the Syncoeliinae, where there are 11–18 so-called testes, there are the usual two vasa efferentia, and the ducts linking these testes to the vasa efferentia are called 'collecting ducts'. The vasa efferentia are of no apparent systematic importance in the Hemiuroidea.

Vas deferens – a duct formed by the fusion of the two vasa efferentia (q.v.), which, in almost all cases, is dilate, filled with spermatozoa and referred to as the seminal vesicle (q.v.). In itself, therefore, it is of no systematic importance, although in certain groups there is a narrow duct linking the seminal vesicle with the pars prostatica (q.v.).

Ventro-cervical groove – a transverse crevice which occurs on the ventral surface immediately anterior to the ventral sucker in many hemiurids. It appears to have no actual function, as it is simply caused by the close proximity of the oral and ventral suckers in some of these genera. The size of this feature appears to be dependent upon the degree of contraction which occurs in the forebody during fixation. It appears to have no systematic value, except that it has occasionally been mistaken for a presomatic pit (q.v.).

Vitellarium – a structure of variable morphology that produces vitelline (yolk) cells which accompany the ovum in egg-formation. The form of the vitellarium is a valuable taxonomic criterion ranging from the species to the family level. The common arrangements of the vitellarium in the Hemiuroidea are as follows (see Fig. 7): (1) follicular; (2) linked follicles, giving a chain-like tubular arrangement; (3) convoluted tubules which are often branched; (4) about seven tubules, usually arranged four on one side of the body and three on the other; (5) about seven oval to digitiform lobes; (6) two oval or slightly lobed masses; and (7) a single oval mass. These forms tend to grade into one another, but it is noticeable that the seven-lobed vitellarium occurs widely throughout the group. The arrangement of the vitellarium is discussed in more detail on p. 124. One unusual feature occurs in the Accacoeliinae, where the sinistral side of the system is reduced to a vestige. In certain instances, especially in the Lecithasteridae and the Derogenidae, the relationship between the vitellarium and the ovary is useful systematically; but the vitellarium or at least the origin of the main vitelline ducts is usually post-ovarian, although exceptions to this include the azygiids and the accacoeliine accacoeliids.

III. A classification of the Hemiuroidea with keys and definitions

Introduction

The following classification, which we propose for the Hemiuroidea, is based upon adult morphology associated with an attempt to understand the function of the organs and organ-systems (see p. 39). This relies heavily upon comparative morphology, as do most of the previous classifications. The main problem with this, as discussed above, is that much of the descriptive work over the years has been inadequate. Many workers around the turn of the century gave detailed and careful descriptions, based upon sectioned material. Work of this standard has been the exception, rather than the rule, since that time. In attempting to provide a feasible classification we have, therefore, examined as many species as possible, both in serial sections and whole-mounts. The lack of certain material has left large gaps, which have had to be filled with a critical appraisal of the literature. In certain groups, and in particular in many individual genera, much of the detail necessary to classify the animals has not been supplied by the original authors. In these cases our classification is particularly tentative, and we have usually indicated where we consider our knowledge to be totally inadequate. In some instances, using our knowledge of the groups as a whole and assessing the functional requirements present, we have assumed the morphology of certain undescribed or apparently wrongly interpreted structures. While this may seem somewhat unsatisfactory, some of our interpretations were proved correct during the course of the work, e.g. before specimens were obtained we correctly assumed the presence of a sinus-sac, rather than a cirrus-sac, in *Arnola* and *Glomericirrus*, and we correctly assumed the presence of Juel's organ in *Elongoparorchis* and in many of the hemiurids (*sensu stricto*).

As far as the systematics of this group is concerned, we have faced many problems in weighing the relative values of different factors. At one time we were inclined to give considerable weight to the details of the terminal genitalia, and also to the vitellarium. While these factors may have significance at the generic or subfamily level, they do seem to be susceptible to development or regression in certain groups. The details of the proximal region of the female system have, we believe, a fundamental value in distinguishing subfamilies, although there are exceptions to this, for in the Derogenidae and the Trifoliovariinae a variety of conditions occur. The presence of Juel's organ, for example, seems to be of considerable importance; but, even in this case, care has to be taken, and the complete morphological pattern must be taken into consideration.

Definitions of the taxa are presented; but features common to a group of taxa are given in the definition of the higher taxa, rather than repeated throughout the group. Features, especially those taken from the literature, which we believe to be questionable, are indicated by question-marks.

Wherever possible material was examined, especially in serial section. The abbreviations used to indicate what material we have seen are given after the generic name, and are as follows: T=type-material of type-species; t=non-type material of type-species; n=material of non-type-species; w=whole-mount; s=serial sections. The absence of this information indicates that the data have been derived from the literature.

We have attempted to provide dichotomous keys to the taxa. Rather than relying upon the most obvious of criteria, we have tried to produce keys which work, with the result that the sectioning of material, while always advisable, may in fact be essential. These keys must be used with care, and with the understanding that this classification is based upon polythetic assemblages of characters. Soft-bodied animals, such as digeneans, give few good metrical or meristic characters, so that it is very important to possess a good understanding of the overall morphology while attempting to determine these worms.

Some readers may note that the authorities which we have given for some of the family-group names differ from those presented by some other workers. These workers appear to have followed a recent trend which tends to confuse systematics and nomenclature. In using the authority for the original mention of the family-group name, irrespective of suffix, we are following Article 36 of the International Code of Zoological Nomenclature.

As with any work of this kind, our classification must be considered provisional. We hope that it may be helpful in stimulating and encouraging a closer and more careful examination of the worms in this group.

Superfamily **HEMIUROIDEA** Looss, 1899

Azygioidea Lühe, 1909
Accacoelioidea Odhner, 1911
Isoparorchioidea Travassos, 1922

Body small to large; oval to cylindrical. Ecsoma present or absent. Body-surface smooth, rugate or plicated (or 'scaley'); never spiny, but occasionally papillate. Oral and ventral suckers well developed, occasionally small. Ventral sucker normally in middle or anterior half of body, occasionally just inside posterior half of body; occasionally pedunculate. Prepharynx absent. Pharynx well developed; normally oval, occasionally modified. Oesophagus usually short, occasionally long. 'Drüsenmagen' present or absent. Gut-caeca usually end blindly near posterior extremity, occasionally form cyclocoel or uroproct. Testes normally two, rarely one or follicular; normally tandem to symmetrical, preovarian and near middle of body; occasionally in forebody or post-ovarian. Seminal vesicle oval to tubular; occasionally constricted into portions usually thin- but occasionally thick-walled; in fore- or hindbody; normally external to sinus-sac, rarely partly or entirely internal. Pars prostatica tubular to vesicular; long or short; normally external to sinus-sac, rarely internal; usually in forebody, occasionally entirely inside, or extending into, hindbody. Ejaculatory duct usually present; usually short; often within sinus-sac or sinus-organ; normally unites with metraterm to form hermaphroditic duct; occasionally within 'cirrus-sac'. Hermaphroditic duct usually present; usually within sinus-sac and/or sinus-organ. Sinus-sac present or absent; oval to cylindrical; normally enclosing ejaculatory duct and part of metraterm and/or hermaphroditic duct; occasionally additionally enclosing ejaculatory (prostatic) vesicle or seminal vesicle and/or pars prostatica. Permanent sinus-organ present or absent within genital atrium; conical to tubular; muscular or non-muscular. Temporary sinus-organ sometimes formed from hermaphroditic duct. 'Cirrus-sac', enclosing ejaculatory duct only, and 'cirrus' rarely present. Genital atrium large, small or absent. Common genital pore mid-ventral in forebody. Ovary usually oval, occasionally lobed, rarely tubular or follicular; usually post-testicular, occasionally pre-testicular, rarely inter-testicular; normally in hindbody, rarely in forebody. Mehlis' gland usually post-ovarian, occasionally pre-ovarian. Uterine seminal receptacle plus Laurer's canal and/or Juel's organ *or* blind seminal receptacle alone normally present. Uterine coils usually fill much of hindbody, occasionally extending well into forebody, rarely entirely in forebody. Eggs normally oval; usually small, numerous; occasionally with spine, filament(s) or threads. Vitellarium normally follicular, tubular or composed of a small number (often *seven*) oval to tubular lobes or one to three (usually two) entire or lobed masses; often post-ovarian, occasionally pre-ovarian; sometimes extending throughout hindbody or into forebody, rarely entirely in forebody. Excretory pore terminal; vesicle Y-shaped; arms united in forebody or not. Manter's organ (accessory excretory vesicle) rarely present. Parasitic in gut, especially stomach, primarily of marine teleosts, but commonly occur in freshwater teleosts and elasmobranchs, occasionally in holosteans, amphibians, reptiles and progenetic in invertebrates; occasionally recorded from gills, skin, body-cavity, swim-bladder and other organs.

Key to Hemiuroidea

1. A. Vitellarium composed of numerous widely distributed follicles (2)
B. Vitellarium otherwise, usually composed of a small number of oval to tubular (occasionally branched) lobes or 1–3 distinct oval, lobed or unlobed masses (3)
2. A. Prostatic sac present; parasitic in elasmobranchs and freshwater teleosts **AZYGIIDAE** (p. 60)
B. Prostatic sac absent; parasitic in gut of elasmobranchs **PTYCHOGONIMIDAE** (p. 110)
3. A. Testes 2, occasionally 1 (4)
B. Testes follicular, 11–18 large or many small follicles arranged in rows or irregularly distributed; usually parasitic in buccal or branchial cavities or on skin (? occasionally internally) of elasmobranchs and marine teleosts **SYNCOELIIDAE** (p. 114)
4. A. Ecsoma absent (take care with this observation as some hemiurids have a reduced ecsoma and some bunocotylids may retain the vestige of an ecsoma) (5)
B. Ecsoma present (sometimes very reduced); body surface often plicated; Juel's organ and uterine seminal receptacle present; vitellarium varies between form with 7 tubular lobes and form with 2 distinct oval masses; parasitic mainly in gut of marine teleosts, occasionally present in freshwater teleosts and lung of sea-snakes **HEMIURIDAE** (p. 84)
5. A. Ovary usually post-testicular, occasionally pre-testicular (6)
B. Ovary inter-testicular; parasitic on gills (? and in stomach) of marine teleosts **BATHYCOTYLIDAE** (p. 62)
6. A. Ovary oval or lobed (7)
B. Ovary tubular; parasitic in swim-bladder of freshwater teleosts **ISOPARORCHIIDAE** (p. 100)
7. A. Ventral sucker anterior to middle of body; parasitic in marine teleosts; seminal vesicle never enclosed in sinus-sac (8)
B. Ventral sucker usually in or near middle of body, occasionally more anterior; significant proportion of uterus usually present in forebody [a small number of marine forms do possess a ventral sucker in the anterior half of the body and uterine coils which do not extend into the forebody, but these forms also possess a seminal vesicle which is enclosed within the sinus-sac]; vitellarium 1 or 2 masses, entire or lobed (lobes normally shallow, rarely digitate); seminal vesicle in forebody; ovary and vitellarium pre- or post-testicular; parasitic mainly in gut of freshwater and marine teleosts, occasionally in amphibians, reptiles and freshwater shrimps **DEROGENIDAE** (p. 71)
8. A. 'Cirrus' present, enclosed in 'cirrus-sac'; female duct opens into genital atrium independently; large parasites from gut (? or gills) of marine teleosts (immature forms occasionally present in salmonids) **HIRUDINELLIDAE** (p. 98)
B. 'Cirrus' and 'cirrus-sac' absent; male and female ducts normally unite forming hermaphroditic duct, which is often present within a sinus-organ and enclosed by a sinus-sac (9)
9. A. Parasitic in gut (occasionally on gills) (10)
B. Parasitic in swim-bladder or gall-bladder (13)
10. A. Vitellarium 1, 2 or 3 compact masses **BUNOCOTYLIDAE** (p. 62)
B. Vitellarium otherwise (11)
11. A. Vitellarium 6–8 (occasionally twice this number) oval to digitiform lobes, often arranged in rosette, occasionally branched; Manter's organ absent; pharynx oval **LECITHASTERIDAE** (p. 101)
B. Vitellarium tubular (filamentous) (12)
12. A. Manter's organ present; pharynx oval **SCLERODISTOMIDAE** (p. 111)
B. Manter's organ absent; pharynx with narrow anterior extension into base of oral sucker; occasionally present on gills; commonly parasitic in sunfish (Molidae) **ACCACOELIIDAE** (p. 57)

13. A. Parasitic in swim-bladder; vitellarium 6–8 oval to digitiform lobes, 2 compact multilobulate masses or 2 acinous groups of follicles . . . . **DICTYSARCIDAE** (p. 81)
B. Parasitic in gall-bladder; vitellarium tubular, dendritic, with anteriorly and posteriorly oriented main collecting ducts situated medially . **SCLERODISTOMOIDIDAE** (p. 114)

Family **ACCACOELIIDAE** Odhner, 1911

Body large or small, commonly elongate. Ecsoma absent. Body-surface smooth, but forebody may be papillate. Oral and ventral suckers well developed. Ventral sucker normally in anterior half of body; may be pedunculate. Pharynx well developed; with narrow anterior extension into base of oral sucker; occasionally modified posteriorly. Oesophagus usually long, occasionally short. 'Drüsenmagen' present. Gut-caeca usually H-shaped; terminate blindly or more commonly form uroproct. Testes two; oblique or in tandem; in hindbody, normally close to middle of body; pre-ovarian. Seminal vesicle thin-walled; tubular; sinuous or convoluted; commonly reaching into hindbody. Pars prostatica tubular; external gland-cells may be delimited. Short ejaculatory duct commonly present within sinus-sac. Hermaphroditic duct present or absent. Sinus-sac and sinus-organ present or absent. Genital atrium present. Ovary oval; post-testicular. Mehlis' gland pre- or post-ovarian; linked to anterior or posterior region of ovary by oviduct. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus extensive; coils entirely or almost entirely in hindbody; usually passes close to posterior extremity before looping forward again. Eggs numerous; small; non-filamented. Vitellarium with one or two main collecting ducts; composed of numerous filamentous tubules (? or occasionally chains of follicles) in various parts of the fore- or hindbody. Excretory vesicle Y-shaped; arms initially in dorsal and ventral fields, united in forebody. Metacercariae usually in coelenterates or ctenophores. Parasitic in gut or occasionally on gills of marine teleosts.

COMMENT The vitellarium of the Paraccacladiinae is typical of many of the primitive hemiuroids, possessing a symmetrical pair of main collecting ducts which branch distally and unite proximally to form a common collecting duct. In the Accacoeliinae, however, it appears that the right half of the vitelline system is reduced to a small vestigial process (or reservoir). The whole of the vitelline system of the latter group, therefore, corresponds to only the left-hand side of the vitellarium in other hemiuroids.

Key to Accacoeliidae

1. A. Oesophagus long and narrow; gut-caeca H-shaped; uroproct present; Mehlis' gland pre-ovarian, linked to anterior region of ovary by oviduct; vitellarium with single main collecting duct and system of branching tubules . . **ACCACOELIINAE** (p. 57)
B. Oesophagus short; gut-caeca not distinctly H-shaped and end blindly; Mehlis' gland post-ovarian, linked to posterior region of ovary by oviduct; vitellarium with symmetrical pair of collecting ducts and system of branching tubules . **PARACCACLADIINAE** (p. 59)

Subfamily **ACCACOELIINAE** Odhner, 1911

Tetrochetinae Looss, 1912, emend. Dollfus, 1935
Accacladiinae Yamaguti, 1958
Orophocotylinae Yamaguti, 1958
Rhynchopharynginae Yamaguti, 1958
Guschanskianinae Skrjabin, 1959

Body usually elongate. Body-surface smooth, but forebody may be papillate. Lateral flanges occasionally present on ventral sucker. Pharynx occasionally modified to form two muscular bulbs (*Rhynchopharynx*). Oesophagus long and thin. Gut caeca H-shaped. Uroproct present. Sinus-sac and sinus-organ present or absent; sinus-sac well or poorly developed when present. Mehlis' gland pre-ovarian; linked by oviduct to anterior region of ovary. Vitellarium filamentous; with single main collecting duct on right and single system of ramifying branches in fore- or hindbody; left-hand system reduced to small process or small ramifying system. Parasitic on gills or in gut of marine teleosts (especially Molidae).

Key to Accacoeliinae

1. A. Well-defined sinus-sac and sinus-organ present . . . (2)
B. Well-defined sinus-sac and sinus-organ absent . . . (5)
2. A. Ectoparasitic on gills; long proboscis-like sinus-organ; strongly developed ventral musculature in hindbody; enormous pars prostatica occupying much of forebody; vitellarium posterior to anterior testis . . . ***ACCACOELIUM***
B. Endoparasitic in gut; short cylindrical or dome-shaped sinus-organ; vitellarium not usually extending posteriorly to ovary . . . (3)
3. A. Pharynx pyriform with anterior extension into base of oral sucker . . . (4)
B. Pharynx with two bulbs and anterior elongate portion ensheathed in glandular posterior process of oral sucker; glandular oesophageal bulb immediately posterior to pharynx; large glandular organ of unknown function at base of peduncle ***RHYNCHOPHARYNX***
4. A. Vitellarium confined to hindbody; ventral sucker on extensible peduncle; pars prostatica relatively short . . . ***ACCACLADIUM***
B. Vitellarium wholly or partly in forebody; ventral sucker sessile or nearly so; pars prostatica long . . . ***ACCACLADOCOELIUM***
5. A. Diffuse muscular region around metraterm; muscular sucker-like pads on antero-dorsal surface . . . ***ODHNERIUM***
B. No sinus-sac detectable; no muscular pads present on antero-dorsal surface . . . (6)
6. A. Vitellarium a tubular branching structure on either side of hindbody; no flange on ventral sucker . . . ***TETROCHETUS***
B. Vitellarium comprising (?) few follicles in four rows between the anterior testis and the base of the peduncle; small flange on ventral sucker . . . ***OROPHOCOTYLE***

ACCACOELIUM Monticelli, 1893 [t(w,s)]

Forebody papillate. Oesophagus reaches to ventral sucker. Ventral sucker on short peduncle. Thick muscular layer in ventral hindbody. Sinus-sac present surrounding base of genital atrium. Sinus-organ long and strongly muscular, frequently extended through genital pore. Enormous pars prostatica and associated gland-cells occupy much of forebody. Vitellarium posterior to anterior testis. Parasitic on gills of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacoelium contortum* (Rudolphi, 1819) [by subsequent designation: Looss, 1899].

ACCACLADIUM Odhner, 1928 [t(w,s)]

Body-surface smooth. Oesophagus reaches to ventral sucker. Ventral sucker on extensible peduncle. Pars prostatica well developed. Sinus-sac surrounding base of genital atrium. Sinus-organ short, cylindrical. Vitellarium between ventral sucker and ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacladium serpentulus* Odhner, 1928 [by original designation].

ACCACLADOCOELIUM Odhner, 1928 [t(w,s); n(w,s)]

Guschanskiana Skrjabin, 1959

Body smooth. Lateral flanges on ventral sucker present or absent. Oesophagus reaches to ventral sucker. Pars prostatica long. Sinus-sac present surrounding base of genital atrium. Sinus-organ short, cylindrical. Vitellarium reaches anteriorly to oral sucker, may extend posteriorly just past ovary but usually not beyond anterior testis; reduced fraction may branch. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacladocoelium nigroflavum* (Rudolphi, 1819) [by original designation].

ODHNERIUM Yamaguti, 1934 [t(w,s)]

Mneiodhneria Dollfus, 1935
Caballeriana Skrjabin & Guschanskaja, 1959

Body-surface smooth, but with muscular sucker-like pads on antero-dorsal surface. Flange-like muscular extensions present on ventral sucker; latter pedunculate. Oesophagus reaches to ventral sucker. Pars prostatica reaches half-way back to ventral sucker. Diffuse muscular region surrounds distal parts of metraterm and genital atrium (may be vestige of sinus-sac). Male duct enters genital atrium from side through small papilla. Vitellarium tubular, extending from pharynx to ovary. Parasitic in intestine of marine teleosts (*Mola*).

Type-species. *Odhnerium calyptrocotyle* (Monticelli, 1893) [by original designation].

Comment. We are using the appellation *Odhnerium* rather than *Mneiodhneria*, despite its similarity to *Odhneria* Travassos, 1921, in accordance with the International Code of Zoological Nomenclature.

OROPHOCOTYLE Looss, 1902

[Inadequately described.] Body-surface smooth. Ventral sucker pedunculate; bears small flange. Oesophagus not reaching to ventral sucker. Pars prostatica short. Sinus-sac not reported. Sinus-organ absent. Vitellarium reported to consist of few (?) follicles in four rows between testes and ventral sucker. Parasitic in intestine of marine teleosts (*Ranzania*).

Type-species. *Orophocotyle planci* (Stossich, 1899) [by original designation].

RHYNCHOPHARYNX Odhner, 1928 [t(w,s)]

Forebody papillate. Ventral sucker pedunculate. Pharynx consisting of two muscular bulbs [the 'pharynx-proper' and the 'Russelblase' (snout-bladder)] and an extended anterior snout ('Russel'), which may be extended through the oral sucker. Oral sucker possesses posterior glandular extension, the snout-sheath ('Russelscheide'), which envelopes the snout. Glandular oesophageal bulb present immediately posterior to pharynx. Oesophagus reaches to ventral sucker. Large glandular organ of unknown function present at base of peduncle. Pars prostatica long. Sinus-sac surrounds base of genital atrium. Sinus-organ small. Vitellarium extends from anterior region of ventral sucker to ovary. Parasitic in intestine of marine teleosts (*Mola*).

Type-species. *Rhynchopharynx paradoxa* Odhner, 1928 [by original designation].

TETROCHETUS Looss, 1912 [t(w,s); n(w,s)]

Paratetrochetus Hanson, 1955

Body-surface smooth. Ventral sucker pedunculate. Oesophagus long. Diverticula present at intestinal bifurcation. Pars prostatica short, straight, narrow. Sinus-sac and sinus-organ absent. Male and female ducts open together into shallow genital atrium. Vitellarium tubular, in hindbody; reduced half may be branched. Parasitic in intestine of medusophagus and carnivorous marine teleosts.

Type-species. *Tetrochetus raynerii* (Nardo, 1833) [by monotypy].

Subfamily **PARACCACLADIINAE** Bray & Gibson, 1977

Body elongate. Body-surface smooth, but with papillae on outer surface of ventral sucker. Ventral sucker on short peduncle. Pharynx extended into base of oral sucker. Oesophagus short, wide. Anterior caecal shoulders small. Gut-caeca terminate blindly near posterior extremity. Pars prostatica elongate, convoluted. Sinus-sac present surrounding base of genital atrium; musculature diffuse. Sinus-organ short, cylindrical. Mehlis' gland post-ovarian; linked to posterior region of ovary by oviduct. Vitellarium with symmetrical pair of main collecting ducts and ramifying systems of tubules; posterior to ovary. Mature forms parasitic in rectum of carnivorous marine teleosts (*Coryphaenoides*); immature forms parasitic in rectum of medusophagus marine teleosts.

PARACCACLADIUM Bray & Gibson, 1977 [T(w,s)]

Defined as subfamily.

TYPE-SPECIES. *Paraccacladium jamiesoni* Bray & Gibson, 1977 [by original designation].

Family **AZYGIIDAE** Lühe, 1909

Aphanhysteridae Guiart, 1938

Body large or small; usually elongate. Ecsoma absent. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; latter in middle or anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' apparently absent. Gut-caeca terminate blindly close to posterior extremity. Testes two; in tandem, oblique or symmetrical; pre- or post-ovarian in hindbody. Seminal vesicle tubular, usually short, thin-walled; convoluted in forebody. Pars prostatica tubular. Prostatic sac present surrounding pars prostatica and seminal vesicle. Ejaculatory duct usually long and convoluted, but of variable length. Hermaphroditic duct short; at distal extremity of sinus-organ. Permanent sinus-organ variable in length; usually conical. Sinus-sac absent. Genital atrium usually well developed; variable in size. Genital pore mid-ventral in forebody. Ovary oval; pre- or post-testicular. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus entirely or almost entirely pre-ovarian; coiled mainly in hindbody. Eggs numerous; small; non-filamented. Vitellarium follicular; usually present laterally throughout much of hindbody; occasionally extending into forebody. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic in stomach or body-cavity of elasmobranchs and in stomach of freshwater teleosts and holosteans.

Key to Azygiidae

1. A. Testes post-ovarian . . . . **AZYGIINAE** (p. 60)
B. Testes pre-ovarian . . . . **LEUCERUTHRINAE** (p. 62)

Subfamily **AZYGIINAE** Lühe, 1909

Aphanhysterinae Guiart, 1938
Gomtiotrematinae Gupta, 1955
Allogomtiotrematinae Yamaguti, 1958
Proterometrinae Yamaguti, 1958

Body normally large; occasionally small. Ventral sucker larger or smaller than oral sucker; in middle or anterior half of body. Testes in tandem, oblique or symmetrical; post-ovarian. Uterus entirely pre-testicular. Vitelline field may extend into forebody. Excretory arms may or may not unite in forebody. Parasitic in stomach or body-cavity of elasmobranchs and stomach of freshwater teleosts and holosteans.

Key to Azygiinae

1. A. Testes symmetrical; vitelline follicles and uterine coils extending into forebody; testes near posterior extremity; in freshwater teleosts (N. America) . . . . ***PROTEROMETRA***
B. Testes tandem, oblique, or occasionally symmetrical; vitelline follicles and uterine coils entirely or almost entirely confined to hindbody; testes usually well anterior to posterior extremity 2
2. A. Vitelline follicles confluent posterior to testes; ventral sucker normally larger than oral sucker; parasitic in elasmobranchs . . . . ***OTODISTOMUM***
B. Vitelline follicles not confluent posterior to testes; oral sucker normally larger than ventral sucker; parasitic in freshwater teleosts and holosteans . . . . . . ***AZYGIA***

AZYGIA Looss, 1899 [t(w,s)]

Megadistomum Stafford, 1904
Mimodistomum Stafford, 1904
Hassallius Goldberger, 1911
Eurostomum MacCallum, 1921
Gomtiotrema Gupta, 1955, *nec* Sinha, 1934
Allogomtiotrema Yamaguti, 1958

Body medium to large; usually elongate, occasionally oval. Ventral sucker smaller than oral sucker; in anterior half of body. Testes tandem, occasionally to symmetrical; anterior testis occasionally lateral to ovary (*A. asiatica*). Sinus-organ a small papilla-like structure. Uterine field between ovary and ventral sucker. Vitelline follicles confined to hindbody; not confluent posterior to testes. Excretory arms apparently not united in forebody. Parasitic in stomach and intestine of freshwater teleosts and holosteans.

Type-species. *Azygia lucii* (Müller, 1776) [by subsequent designation: Goldberger, 1911*a*].

Comment. Yamaguti (1971) recognizes two subgenera, *Azygia* Looss, 1899, and *Pseudazygia* Yamaguti, 1971. He distinguishes these by the length of the post-testicular region and the position of the bifurcation of the excretory vesicle. The former criterion appears to be a somewhat variable feature in *Azygia asiatica* Simha & Pershad, 1964, and in *A. angusticauda* (Stafford) of Kakaji (1968; ? synonym of *A. asiatica*).

OTODISTOMUM Stafford, 1904 [t(w,s); n(w,s)]

Xenodistomum Stafford, 1904
Josstaffordia Odhner, 1911*
Aphanhystera Guiart, 1938

Body large; spatulate to elongate. Ventral sucker larger than oral sucker; close to anterior extremity. Testes tandem or slightly oblique. Sinus-organ capable of considerable extension or contraction to form small papilla. Uterine field almost entirely between ovary and ventral sucker. Vitelline follicles extend in lateral fields posterior to ventral sucker, reaching back to post-testicular region where fields are confluent. Excretory arms usually unite in forebody, but occasionally do not. Parasitic in stomach or body-cavity of elasmobranchs (sharks, rays and chimaeras).

Type-species. *Otodistomum veliporum* (Creplin, 1837) [by monotypy].

Comment. It is worth noting that there are two body-forms present in this genus, which appear to be related to their location within the host. The species parasitic within the body-cavity tend to be broad or spatulate, whilst those parasitic in the stomach are very elongate. It is possible that the spatulate body-shape has been evolved to prevent these parasites being lost through the abdominal pores, and it is noticeable that the gorgoderid and monogenean parasites from the body-cavity of elasmobranchs are also spatulate or oval. Elasmobranchs are the only group of vertebrates which commonly harbour adult helminths in the body-cavity: this is because the abdominal pores form an exit for the release of eggs. The excretory arms in species of *Otodistomum* are normally considered to unite in the forebody; but in sectioned material of *O. plunketi* Fyfe, 1953, they end blindly (Gibson & Bray, 1977).

PROTEROMETRA Horsfall, 1933

Body oval; small. Oral sucker large; ventral sucker small, situated at or just posterior to middle of body. Testes symmetrical at posterior extremity. Sinus-organ a small cone. Uterine field extends from ovary into forebody. Vitellarium extends from level of testes or ovary anteriorly well into forebody, in lateral fields. Excretory arms united in forebody. Parasitic in gut of freshwater teleosts (in North America).

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* The appellation *Josstaffordia josstaffordi* n.g., n.sp. was proposed by Odhner (1911) for specimens of *Otodistomum* in a sarcastic footnote, mimicking the erection of *Hassallius hassalli* by Goldberger (1911a). Although he gives indications as to its distinctive features, it is obvious that Odhner did not intend it to be considered valid.

TYPE-SPECIES. *Proterometra macrostoma* (Faust, 1918) [by monotypy].

Subfamily **LEUCERUTHRINAE** Goldberger, 1911

Body medium to large; elongate oval. Ventral sucker smaller than oral sucker; near middle of body. Testes oblique; pre-ovarian; immediately posterior to ventral sucker. Prostatic sac small. Sinus-organ small, but well defined. Uterine field between ovary and ventral sucker, passing between testes. Vitelline follicles in lateral fields, extending almost throughout length of hindbody. Excretory arms unite in forebody. Parasitic in gut of freshwater teleosts and holosteans (in North America).

LEUCERUTHRUS Marshall & Gilbert, 1905

Defined as subfamily.

TYPE-SPECIES. *Leuceruthrus micropteri* Marshall & Gilbert, 1905 [by monotypy].

Family **BATHYCOTYLIDAE** Dollfus, 1932

Body large; elongate, but stout. Ecsoma absent. Body-surface smooth, but may be wrinkled. Oral and ventral suckers well developed; latter just in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present. Gut-caeca end blindly close to posterior extremity. Testes two; tandem; separated by ovary; in mid-hindbody. Seminal vesicle thin-walled; tubular; convoluted; small; well forward in forebody. Pars prostatica tubular; indistinct. Sinus-organ and sinus-sac absent. Genital atrium small, but deep. Genital pore mid-ventral close to posterior margin of oral sucker. Ovary oval to reniform; inter-testicular. Mehlis' gland posterior or lateral to ovary. Laurer's canal [see below] and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus fills much of hind- and forebody. Eggs numerous; small; non-filamented. Vitellarium several filamentous tubules in hindbody. Excretory vesicle Y-shaped; arms united in forebody. Parasitic on gills (? or in stomach) of pelagic marine teleosts (scombrids and *Coryphaena*).

BATHYCOTYLE Darr, 1902 [n(w,s)]

Defined as family.

TYPE-SPECIES. *Bathycotyle branchialis* Darr, 1902 [by monotypy].

COMMENT. Although Yamaguti (1938*a*) states: 'Laurer's canal apparently without external opening', when describing *Bathycotyle coryphaenae* Yamaguti, 1938, it is obvious that a dorsal pore does occur in the type-species, as Dollfus (1932) clearly illustrated it in his figure 5. Yamaguti, however, in contrast to Dollfus, apparently failed to section his material.

Family **BUNOCOTYLIDAE** Dollfus, 1950

Body usually small; fusiform to elongate. Distinct ecsoma absent, but vestige may remain. Body-surface smooth or with plications. Ridges around body often present at level of oral sucker and posterior margin of ventral sucker. Ventral sucker normally inside anterior half of worm. Pharynx well developed. Oesophagus normally short. 'Drüsenmagen' normally present. Gut-caeca normally end blindly near posterior extremity or occasionally form cyclocoel. Testes two; pre-ovarian in hindbody; tandem to symmetrical. Seminal vesicle saccular or tubular; in fore- or hindbody. Pars prostatica tubular or vesicular; short or long; may extend into hindbody. Ejaculatory duct long, short or apparently absent. Sinus-sac usually present, occasionally absent. Hermaphroditic duct present; within sinus-sac when latter present. Permanent sinus-organ normally absent, but temporary sinus-organ may form. Genital atrium small or absent. Ovary oval; rarely bilobed; between testes and vitellarium. Mehlis' gland post-ovarian. Laurer's canal and canalicular seminal receptacle absent. Juel's organ and uterine seminal receptacle present or absent. Blind seminal receptacle present or absent. Uterus normally almost entirely in hindbody; mainly pre- to mainly post-ovarian. Eggs numerous; small; without filaments. Vitellarium one or two, occasionally three, entire (rarely slightly lobed) masses; posterior or postero-lateral to ovary. Excretory arms rarely fail to unite in forebody; stem of excretory vesicle often with terminal bulb or with large pore (actual pore may be withdrawn within vestige of ecsoma). Parasitic mainly in stomach of marine teleosts.

Key to Bunocotylidae

1. A. Uterine seminal receptacle present; vitellarium 1 or 2 masses 2
B. Blind seminal receptacle present; body-surface smooth; vitellarium 2 or 3 masses **OPISTHADENINAE** (p. 66)
2. A. Parasites up to 6 mm in length; large concentration of uterine coils between ovary and testes . . . . **THELETRINAE** (p. 69)
B. Parasites small, rarely more than 2 mm in length, commonly less than 1 mm; large concentration of uterine coils not present between ovary and testes 3
3. A. Body-surface smooth; ridges present around body at level of oral sucker and posterior margin of ventral sucker; major part of uterine field pre-ovarian; vitellarium single **BUNOCOTYLINAE** (p. 63)
B. Body-surface usually plicated, occasionally smooth; ridges around body at level of sucker absent; large or major part of uterine field post-ovarian; vitellarium single or double **APHANURINAE** (p. 64)

Subfamily **BUNOCOTYLINAE** Dollfus, 1950

Body small. Vestige of ecsoma may be present. Body-surface smooth. Ridges present around body at level of oral sucker and posterior margin of ventral sucker; additional ridge often present close to posterior extremity. Transverse septate partitions of body may occur. Gut-caeca end blindly or form cyclocoel. Testes tandem to oblique; not separated from ovary by large concentration of uterine coils. Seminal vesicle saccular; oval to elongate; in forebody or dorsal to ventral sucker. Pars prostatica short; tubular or vesicular. Sinus-sac absent or small and tubular to oval. Short hermaphroditic duct may extend to form temporary sinus-organ. Genital atrium absent or small. Ovary oval. Uterine seminal receptacle present (?). Juel's organ not reported. Blind seminal receptacle absent. Vitellarium a single, unlobed mass; immediately post-ovarian. Excretory vesicle expanded distally; arms united in forebody; pore wide. Parasitic in gut of freshwater and euryhaline teleosts; occasionally progenetic in snails and copepods.

Comment. According to the literature, the type of seminal storage apparatus occurring in this subfamily is a matter of some disagreement. Manter (1969*a*) observed a uterine seminal receptacle in *Saturnius segmentatus* Manter, 1969, whereas Yamaguti (1970) described a seminal receptacle in *S. mugilis* (Yamaguti, 1970). Overstreet (1977), when re-defining *Saturnius*, stated that a seminal receptacle was absent. No seminal storage apparatus has been described for *Bunocotyle cingulata* Odhner, 1928, by Odhner (1928*b*) or for *B. progenetica* (Markowski, 1936) by Deblock (1975). We have examined sections of a paratype specimen of *Saturnius papernai* Overstreet 1977, and confirm that: (1) a distinct seminal receptacle (canalicular or blind) and Laurer's canal are absent; and (2) spermatozoa are present in the proximal region of the uterus, which thus functions as a uterine seminal receptacle. We could not for certain distinguish Juel's organ, but it is possible that in the small species which constitute this subfamily, this structure is reduced or lost altogether.

It is conceivable that the transverse ridge around the posterior extremity in some species of this subfamily, and possibly both the ampullaceous nature of the distal region of the stem of the excretory vesicle and the wide excretory pore, represent vestiges of an ecsoma. Overstreet (1977) has described the former as a possible small ecsoma in *S. maurepasi* Overstreet, 1977, where, in the living worm, it may be partly withdrawn.

Key to Bunocotylinae

1. A. Transverse fibrous septa in fore- and hindbody; cyclocoel absent; sinus-sac present; parasitic in euryhaline teleosts *(Mugil)* . . . . ***SATURNIUS***

B. Transverse septa not present; cyclocoel present; sinus-sac absent; parasitic in freshwater or euryhaline teleosts, or progenetic in snails and copepods . . ***BUNOCOTYLE***

BUNOCOTYLE Odhner, 1928

Transverse fibrous septa absent. Cyclocoel present. Sinus-sac absent. Uterine seminal receptacle (?) presumed to be present. Parasitic in gut of freshwater or euryhaline teleosts, or progenetic in snails and copepods.

Type-species. *Bunocotyle cingulata* Odhner, 1928 [by original designation].

Comment. See *Theletrum* for comment on *B. sudatlantica* Parukhin, 1976.

SATURNIUS Manter, 1969 [n(w,s)]

Small papillae or corrugations may be associated with suckers. Internal transverse, fibrous septa present in fore- and hindbody. Gut-caeca end blindly. Sinus-sac may contain ejaculatory (? hermaphroditic) vesicle. Parasitic in, and under lining of, stomach of euryhaline teleosts (*Mugil cephalus*).

Type-species. *Saturnius segmentatus* Manter, 1969 [by original designation].

Comment. This genus has recently been revised by Overstreet (1977), who has cleared up many of the discrepancies between the descriptions of *S. segmentatus* and *S. mugilis* (Yamaguti, 1970).

Subfamily **APHANURINAE** Skrjabin & Guschanskaja, 1954 [28.4.1954]

Ahemiurinae Chauhan, 1954 [17.11.1954]

Body normally small. Vestige of ecsoma may be present. Body-surface usually with distinct annular plications, occasionally (?) smooth [some species of *Aphanurus*]. Ridges around body at level of suckers absent. Gut-caeca end blindly near posterior extremity. Testes tandem to symmetrical; normally well posterior to ventral sucker; not separated from ovary by large concentration of uterine coils. Seminal vesicle tubular in forebody, or saccular (oval, elongate or bipartite) in hindbody (or at least posterior to middle of ventral sucker). Pars prostatica tubular or vesicular; short or long. Ejaculatory duct long, short or apparently absent. Sinus-sac present, enclosing hermaphroditic duct, or (?) absent. Ovary oval; immediately or almost immediately post-testicular. Blind seminal receptacle absent. Uterine seminal receptacle and (?) Juel's organ present. Large or major part of uterine field post-ovarian. Vitellarium one or two compact masses; usually immediately posterior, occasionally lateral, to ovary. Excretory arms united in forebody; excretory pore often large; actual pore may be withdrawn within vestige of ecsoma. Parasitic mainly in stomach or oesophagus of marine teleosts.

Comment. A small 'seminal receptacle' has been reported for *Duosphincter* by Yamaguti (1970) and in some species of *Aphanurus*. A uterine seminal receptacle has been reported for *Myosaccium* and other species of *Aphanurus*. It is likely that the reports of a 'seminal receptacle' from this group are mistaken, as Juel's organ and a uterine seminal receptacle are easily mistaken for such a structure in whole-mount preparations.

The genera of this group are essentially typical hemiurids which have lost their ecsoma. The presence of records from the oesophagus suggests that these parasites may inhabit the less acidic anterior regions of the stomach, and do not have the same requirement for an ecsoma as the closely related forms which tend to inhabit the pyloric region of the stomach.

Key to Aphanurinae

1. A. Vitellarium composed of 2 distinct masses 2
B. Vitellarium composed of 1 distinct mass . . . . ***APHANURUS***
2. A. Seminal vesicle tubular, winding in forebody . . . . . . ***DUOSPHINCTER***
B. Seminal vesicle saccular (oval, elongate or bipartite; often attenuated anteriorly), posterior to middle of ventral sucker 3
3. A. Pars prostatica vesicular, with muscular wall . . . . . . ***MYOSACCIUM***
B. Pars prostatica tubular 4
4. A. Seminal vesicle oval; sinus-sac present . . . . ***AHEMIURUS***
B. Seminal vesicle apparently bipartite and attenuated anteriorly; sinus-sac apparently absent ***APHANUROIDES***

APHANURUS Looss, 1907 [n(w)]

Chauhanurus Skrjabin & Guschanskaja, 1954
Helaphanurus Slusarski, 1957

Body-surface normally plicated, occasionally (?) smooth. Testes oblique, occasionally symmetrical or tandem. Seminal vesicle oval to elongate oval; in hindbody; wall may be muscular. Pars prostatica tubular; long. Ejaculatory duct long or short. Sinus-sac present; tubular. Temporary sinus-organ sometimes present as small cone. Vitellarium a single, large, entire or slightly indented, post-ovarian mass. Parasitic in oesophagus and stomach of essentially marine teleosts from marine and brackish water environments.

Type-species. *Aphanurus stossichi* (Monticelli, 1891) [by original designation].

Comment. There has been considerable comment in the literature (Looss, 1908; Rioja, 1923; Chauhan, 1954; Slusarski, 1957) as to whether *Aphanurus* possesses or lacks a small vestigial ecsoma. Although this question has not been resolved, Chauhan (1954) suggested that the confusion may have been caused by the bulbous nature of the excretory vesicle. The possible vestiges of an ecsoma, however, may be a common feature of both the aphanurines and the bunocotylines. Some species of *Aphanurus* (*A. caesionis* Yamaguti, 1952 and *A. dorosomatis* Yamaguti, 1953) are reported to have a smooth body-surface; but, as they are known from only one or two specimens, this requires confirmation. If this is proved to be correct, then there may be grounds for distinguishing them from the other species of *Aphanurus* at the generic level.

AHEMIURUS Chauhan, 1954

Testes symmetrical to oblique. Seminal vesicle oval; in hindbody. Pars prostatica tubular; long. Ejaculatory duct long. Sinus-sac present; elongate oval. Vitellarium two oval, compact masses; symmetrical; post-ovarian. Parasitic in stomach of marine teleosts.

Type-species. *Ahemiurus karachii* (Srivastava, 1937) [by original designation].

Comment. Yamaguti (1971) lists *Ahemiurus* as a synonym of *Opisthadena* despite the fact that Chauhan (1954) emphasized the presence of cuticular plications in this species. The latter is a feature which occurs only in hemiurid and aphanurine genera. Although the seminal storage apparatus of the genus has not been described, we expect it to conform to the subfamily definition.

(?) ***APHANUROIDES*** Nagaty & Abdel-Aal, 1962

[Inadequately described.] Testes tandem. Seminal vesicle saccular; (?)bipartite; attenuated anteriorly; extending between anterior testis and posterior half of ventral sucker. Pars prostatica tubular. [Terminal genitalia not described in detail.] Sinus-sac (?) absent. Short hermaphroditic duct and genital atrium apparently present. [Figures of Nagaty & Abdel-Aal, 1962, suggest that temporary sinus-organ may form (?).] Vitellarium two compact masses; symmetrical to oblique; post-ovarian. Excretory arms (?). Parasitic in gut of marine teleosts.

TYPE-SPECIES: *Aphanuroides lethrini* Nagaty & Abdel-Aal, 1962 [by original designation].

DUOSPHINCTER Manter & Pritchard, 1960

Strongly developed sphincter muscles surround apertures of suckers. Testes oblique to tandem. Seminal vesicle tubular; winding in forebody. Pars prostatica tubular; short. Sinus-sac small; oval. Temporary sinus-organ may form. [Small seminal receptacle (? Juel's organ) present, according to Yamaguti, 1970.] Vitellarium two oval masses; oblique to tandem; immediately post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Duosphincter zancli* Manter & Pritchard, 1960 [by monotypy].

MYOSACCIUM Montgomery, 1957

Neogenolinea Siddiqi & Cable, 1960.

Testes symmetrical to tandem. Seminal vesicle saccular; attenuated anteriorly; at level of posterior margin of ventral sucker. Pars prostatica vesicular; with strong, muscular wall; in forebody. [Terminal genitalia confused in literature.] Sinus-sac apparently tubular; enclosing hermaphroditic duct, which may form temporary sinus-organ. Eggs without filament [the structure of collapsed eggs may apparently give the impression that a short filament and spine are present (?)]. Vitellarium two oval or slightly indented masses; oblique to tandem; one mass usually lateral, other immediately postero-lateral or posterior, to ovary. Parasitic in stomach of marine teleosts (Clupeidae).

TYPE-SPECIES. *Myosaccium ecaude* Montgomery, 1957 [by original designation].

COMMENT. There appears to be some difference of opinion with regard to the presence or absence of filaments on the eggs. Montgomery (1957) and Kohn & Bührnheim (1964) indicate that a filament is present with, in the case of the latter authors, an additional small spine at the opposite end of the egg. Overstreet (1969) and Yamaguti (1971), after examining some of Montgomery's type-specimens, state that filaments on the egg could not be seen. Overstreet suggests that the so-called filaments described in this genus may be an artifact present in collapsed eggs.

Subfamily **OPISTHADENINAE** Yamaguti, 1970

Intuscirrinae Skrjabin & Guschanskaja, 1959

Body spindle-shaped to elongate. Body-surface smooth. Transverse ridges in body-wall present or absent around body at level of oral sucker and/or posterior margin of ventral sucker [these are often not obvious]. Presomatic pit reported (?) in *Mitrostoma*. Gut-caeca end blindly near posterior extremity. Testes tandem to oblique; usually well posterior to ventral sucker and near ovary; not separated from ovary by large concentration of uterine coils. Seminal vesicle tubular to saccular (? rarely bipartite); in fore- or hindbody. Pars prostatica long or short; tubular or vesicular. Ejaculatory duct long to short or apparently absent. Sinus-sac present; oval to elongate oval; enclosing hermaphroditic duct. Sinus-organ (? temporary) occasionally present. Genital atrium usually present; small. Ovary normally oval, occasionally bilobed; normally close to testes. Blind seminal receptacle present; large; usually dorsal or antero-dorsal to ovary. Juel's organ and uterine seminal receptacle absent. Uterus mainly pre- to mainly post-ovarian. Vitellarium two, occasionally three, entire or slightly indented masses; posterior or postero-lateral to ovary. Excretory arms usually, but not always, united in forebody. Parasitic in stomach, occasionally intestine, of marine teleosts.

COMMENT. The presence of ridges (tegumental folds) around the body, especially the one immediately posterior to the ventral sucker, may well be a good generic criterion. We are concerned about the significance of this feature, as it is often very difficult to see, and in genera such as *Genolinea*, where it is known to occur, it has only been reported occasionally.

Key to Opisthadeninae

1. A. Seminal vesicle entirely in hindbody 2
   B. Seminal vesicle in forebody (occasionally dorsal or postero-dorsal to ventral sucker) . 3
2. A. Ejaculatory duct short or absent; pars prostatica reaches forward to level of caecal bifurcation; (?) presomatic pit apparently present . . . . *MITROSTOMA*
   B. Ejaculatory duct long; pars prostatica does not reach further forward than ventral sucker; presomatic pit absent . . . . *OPISTHADENA*
3. A. Vitellarium 2 symmetrical, oblique or tandem masses . . . . . . *GENOLINEA*
   B. Vitellarium 3 masses, the anterior pair being symmetrical and the posterior mass being the largest . . . . *NEOTHELETRUM*

OPISTHADENA Linton, 1910

Body elongate. Transverse ridge (fold) of body-wall around body immediately posterior to ventral sucker. Testes tandem; posterior to middle of body. Seminal vesicle in hindbody; usually tubular and sinuous, but reported as enclosed within muscular, ovoid sac ['seminal sac' of Manter, 1947] or as being saccular. Pars prostatica tubular; not reaching further forward than posterior margin of ventral sucker. Ejaculatory duct long. Sinus-sac oval. Hermaphroditic duct may be sub-divided. Sinus-organ apparently present as small cone, at least temporarily. Ovary close to testes. Uterus mainly pre-ovarian. Vitellarium two symmetrical to oblique masses; post-ovarian. Excretory arms diverticulate; united in forebody. Parasitic in stomach of marine teleosts (especially *Kyphosus*).

TYPE-SPECIES. *Opisthadena dimidia* Linton, 1910 [by original designation].

GENOLINEA Manter, 1925 [t(w,s); n(w,s)]

Parasterrhurus Manter, 1934
Intuscirrus Acena, 1947
Pseudobunocotyla Yamaguti, 1965

Body spindle-shaped to slightly elongate. Transverse ridge usually present around body immediately posterior to ventral sucker (often inconspicuous and frequently not reported); similar ridge may surround oral sucker. Large pre-oral lobe may be present. Ventral sucker normally in anterior half of body, (?) occasionally near middle; sphincter muscles sometimes present around aperture. Testes tandem to oblique; close to ovary. Seminal vesicle small; tubular; convoluted in forebody, occasionally dorsal or postero-dorsal to ventral sucker. Pars prostatica tubular to vesicular; short. Ejaculatory duct short or absent. Sinus-sac oval to elongate oval; small. Sinus-organ occasionally present (? temporary). Ovary near middle of hindbody. Uterus usually in both pre- and post-ovarian fields, occasionally post-vitelline distribution is limited. Metraterm reported in some instances to be spinous (?). Vitellarium two compact (occasionally lobed), symmetrical, oblique or tandem masses; posterior or postero-lateral to ovary. Excretory arms united in forebody. Parasitic mainly in stomach of marine teleosts.

TYPE-SPECIES. *Genolinea laticauda* Manter, 1925 [by original designation].

COMMENT. The position of the ventral sucker near the middle of the body in *G. dactylopagri* Manter, 1954, is much further posterior than normally occurs in this family. The morphology of this species suggests that it is related to *Leurodera* Linton, 1910, as Manter (1954) initially believed, and both are recorded from related percoid families of teleosts.

MITROSTOMA Manter, 1954

Body elongate. Thickened projection present on each side of body at level of posterior margin of ventral sucker. Nipple-shaped protuberance (? vestige of ecsoma) may be present at posterior extremity. Weakly muscled pre-oral lobe bears mouth. Structure resembling (?) presomatic pit apparently present anterior to ventral sucker. Ventral sucker with 'sphincter muscles in anterior and posterior halves'. Testes tandem; close to ovary; near middle of hindbody. Seminal vesicle tubular; convoluted; entirely in hindbody. Pars prostatica tubular; reaches forward to caecal bifurcation. Ejaculatory duct short or absent. Sinus-sac short; pyriform; (?) protrusible. Ovary in posterior half of hindbody. Uterus mainly pre-ovarian, but does extend into post-vitelline region. Vitellarium two oblique to symmetrical, post-ovarian masses. Excretory arms united in forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Mitrostoma nototheniae* Manter, 1954 [by original designation].

COMMENT. There are several features of the genus *Mitrostoma*, such as the overall arrangement of the organs, the apparent presence of a presomatic pit and the reported presence of a nipple-shaped protuberance at the posterior extremity of one specimen, which suggests that it might be a hemiurid with a lost or vestigial ecsoma, no longer required because of its intestinal habitat. Manter (1954), however, reported that a blind seminal receptacle was present. The presence of this type of seminal receptacle, as opposed to a uterine seminal receptacle, and the great morphological similarity between this parasite and *Genolinea bowersi* (Leiper & Atkinson, 1914), reported from related nototheniid hosts (Prudhoe & Bray, 1973), indicate that its position within the Opisthadeninae is probably correct.

NEOTHELETRUM gen. nov.

Body small; elongate to spindle-shaped. Tegumental fold around body posterior to ventral sucker apparently absent. Body-surface smooth. Ventral sucker in anterior half of body. Pre-pharynx absent. Pharynx well developed. Oesophagus short; often with small diverticulum. Gut-caeca end blindly near posterior extremity. Testes 2; oval; oblique to symmetrical; usually separated from ventral sucker by loops of uterus; occasionally sandwiched between ventral sucker and ovary. Seminal vesicle small; tubular to saccular (? occasionally bipartite); in forebody. Pars prostatica short; tubular to vesicular. Ejaculatory duct short or absent. Sinus-sac small; oval. Small temporary sinus-organ may form. Hermaphroditic duct short; formed within sinus-sac. Genital atrium small. Genital pore mid-ventral in forebody. Ovary oval (may occasionally be bilobed); post-testicular; near middle of hindbody. Blind seminal receptacle antero-dorsal to ovary. Laurer's canal, Juel's organ and both canalicular and uterine seminal receptacle presumably absent. Uterus almost entirely in hindbody; usually with roughly equal amounts in pre- and post-ovarian fields; occasionally with majority of uterus in post-ovarian field. Eggs small; numerous; without filaments. Vitellarium three compact, entire or slightly indented masses; anterior pair symmetrical, connected by narrow isthmus; posterior mass larger, may be slightly bilobed [vitellarium is essentially two tandem masses, the anterior of which is divided into two distinct lobes: the vitellarium may appear as two tandem masses in lateral view]; post-ovarian. Excretory arms united in forebody or not. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Neotheletrum lissosomum* (Manter, 1940) n. comb.

COMMENT. *Neotheletrum* differs from *Theletrum* in that: (1) a blind rather than a uterine seminal receptacle is present; (2) much of the uterus is post-ovarian rather than being between the ovary and testes; (3) the anterior vitelline mass is consistently divided into two; and (4) the tegumental ridge around the body immediately posterior to the ventral sucker is absent.

The additional species which we include in this genus are as follows:

N. frontilatum (Manter, 1969) n. comb.
N. gravidum (Manter, 1940) n. comb.
N. magnasaccum (Sogandares-Bernal & Sogandares, 1961) n. comb. [possibly a synonym of *N. lissosomum*].
N. pomacentri (Nahhas & Cable, 1964) n. comb.

N. frontilatum, which Yamaguti (1971) considers to belong to *Hysterolecithoides*, differs from the other species of *Neotheletrum* in that the uterus is almost entirely post-ovarian, the testes are close behind the ventral sucker and close to the ovary, and the excretory arms are not united in the forebody. On these grounds a case could be made for erecting a new genus for this species; but we have included it in *Neotheletrum* as there seems little point in further sub-division at present.

THELETRINAE subfam. nov.

Body elongate. Ecsoma absent. Body-surface smooth; papillae may be present ventrally in fore- or hindbody; transverse ridge may be present around body near posterior margin of ventral sucker and possibly around oral sucker. Oral and ventral suckers well developed; ventral sucker in anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. Gut-caeca end blindly near posterior extremity, (?) or at level of ovary. Testes two; pre-ovarian; tandem to oblique; near middle of hindbody; separated from ovary by majority or large part of uterine coils. Seminal vesicle tubular or (?) saccular; in forebody, but sometimes reaching back to posterior margin of ventral sucker. Pars prostatica short; tubular or slightly vesicular. Ejaculatory duct short or apparently absent. Sinus-sac usually small; oval or elongate oval; weakly developed; enclosing hermaphroditic duct; may extrude slightly through genital pore. Permanent sinus-organ absent (?), but temporary sinus-organ may form. Genital atrium small or absent. Ovary oval; near posterior extremity or at least well inside posterior half of hindbody. Laurer's canal and both canalicular or blind seminal receptacle absent [Laurer's canal reported present (?) in *Indoderogenes*]. Uterine seminal receptacle present. Juel's organ assumed to be present. Uterus almost entirely or mainly in hindbody (small part of uterus is coiled in forebody of *Monolecithotrema*); mainly pre-ovarian, with large proportion of uterine coils between ovary and testes. Eggs numerous; small; without filaments. Vitellarium one entire or two tandem to oblique, entire or slightly lobed masses; posterior or postero-lateral to ovary. Excretory vesicle Y-shaped; arms united in forebody. Parasitic normally in stomach of marine teleosts.

COMMENT. This subfamily is erected for forms which resemble the Opisthadeninae; but lack a blind seminal receptacle, possess a uterine seminal receptacle (plus presumably Juel's organ) and contain a large concentration of uterine coils between the ovary and testes. The position of *Indoderogenes* Srivastava, 1937, discussed below, is problematical; but in gross morphology it does appear to key satisfactorily to this subfamily.

The sinus-sac in both *Theletrum* and *Monolecithotrema* often appears to be slightly extruded through the genital pore. It is not clear from our observations of the type-species if this is in fact so, or whether a temporary sinus-organ is formed by an eversion of the hermaphroditic duct.

Key to Theletrinae

1. A. Vitellarium single (great care should be taken with this observation, as at certain angles the vitellarium of *Theletrum* appears to be single); transverse ridge posterior to ventral sucker absent; some uterine coils in forebody . . . . ***MONOLECITHOTREMA***
   B. Vitellarium double; uterus not coiled in forebody 2
2. A. Seminal vesicle tubular; transverse ridge normally present posterior to ventral sucker; gut-caeca terminate near posterior extremity . . . . . . ***THELETRUM***
   B. Seminal vesicle saccular; transverse ridge posterior to ventral sucker not reported; gut-caeca apparently terminate at level of anterior margin of ovary. . ***INDODEROGENES***

THELETRUM Linton, 1910 [t(w)]

Transverse tegumental ridge present around body immediately posterior to ventral sucker and possibly around oral sucker. Papillae may be present ventrally in hindbody. Gut-caeca terminate at posterior extremity. Testes fairly close together, but separated by uterus. Seminal vesicle tubular. Pars prostatica slightly vesicular. Sinus-sac elongate oval; thin-walled; sheath-like; may be partly extruded through genital pore. Ovary close to posterior extremity. Uterine coils entirely or almost entirely in hindbody; few or no coils posterior to vitellarium. Vitellarium two oblique, entire or slightly lobed masses; close together; posterior or postero-lateral to ovary; at posterior extremity of body. Parasitic in stomach (occasionally intestine) of marine teleosts.

TYPE-SPECIES. *Theletrum fustiforme* Linton, 1910 [by original designation].

COMMENT. We agree with Yamaguti (1971) that this genus is monospecific. We do not agree, however, that the remainder of the species allocated to this genus should be placed in *Genolinea* Manter, 1925, and have, therefore, erected a new genus, *Neotheletrum*, in the Opisthadeninae to accommodate them (see p. 68). Our observations of the type-species confirm that a uterine seminal receptacle is present as indicated by Yamaguti's (1971) and possibly Vigueras' (1958) figures. *Bunocotyle sudatlantica* Parukhin, 1976, may belong to this genus, as it possesses many morphological similarities and is recorded from the same family of host (Chaetodontidae). Parukhin's (1976*a*) description, however, indicates that there is a single vitelline mass and a cyclocoel present. Nevertheless, when viewed from certain angles *T. fustiforme* can appear to possess only one vitelline mass, and the presence or absence of a cyclocoel is often difficult to ascertain in this family. Certainly, Parukhin's material does not fit within our concept of *Bunocotyle*.

(?) ***INDODEROGENES*** Srivastava, 1937

Transverse ridge around body posterior to ventral sucker apparently absent. Gut-caeca terminate close to anterior margin of ovary. Testes separated by uterine coils. Seminal vesicle saccular (flask-shaped). Pars prostatica tubular. Sinus-sac (?) absent. Hermaphroditic duct short. Sinus-organ small (? temporary). Genital atrium small. Ovary close to posterior extremity. Laurer's canal reported present (?). Uterine coils entirely or almost entirely in hindbody; entirely or almost entirely pre-ovarian. Vitellarium two tandem to oblique masses; posterior or postero-lateral to ovary; at posterior extremity of body. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Indoderogenes purii* Srivastava, 1937 [by monotypy].

COMMENT. This genus, initially defined in an abstract by Srivastava (1937*b*) and later (1941) described in more detail, is known from only three specimens. In gross morphology it appears similar to the other two genera of this subfamily, although Srivastava (1941) reported the presence of Laurer's canal. We have some doubts about this, as such an observation on whole-mounts with a large, dense uterine field, as his figure indicates, must be questionable. Despite the fact that no mention was made by Srivastava of the presence of a sinus-sac, there may have been one present, as this structure is either small or weakly developed in the other genera of this subfamily.

If Laurer's canal is proved to be present by future workers, this genus should be transferred to the Halipeginae Poche, 1926, where, although sharing some of its features with *Deropegus* McCauley & Pratt, 1961, its gross morphology does not conform to the normal derogenid pattern. In addition, unlike the majority of halipegines this genus was recorded from a marine teleost, although the locality of the record, an almost land-locked bay in the Bay of Bengal, is brackish at certain times of the year.

MONOLECITHOTREMA Yamaguti, 1970 [T(w)]

Transverse ridges around body absent. Papillae may be present ventrally in forebody. Gut-caeca terminate blindly at posterior extremity. Testes close together, but sometimes separated by uterus. Seminal vesicle tubular; usually extending back dorsally to ventral sucker. Pars prostatica tubular; poorly developed; linked to seminal vesicle by aglandular duct. Sinus-sac small; poorly developed; may be slightly extruded through genital pore. Ovary well inside posterior half of hindbody. Small proportion of uterus may be coiled in forebody; small part of uterus extends posteriorly to vitellarium. Vitellarium one large, entire mass; immediately post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Monolecithotrema kala* Yamaguti, 1970 [by original designation].

COMMENT. Examination of 14 paratype-specimens mounted on a single slide shows that a uterine seminal receptacle is present, and that Yamaguti was probably mistaken in his observation of a small seminal receptacle between the ovary and the vitellarium. This structure corresponds with the position of Mehlis' gland, but might also have been part of the uterine seminal receptacle, Juel's organ (until sectioned material is examined we are assuming that this is present) or even a diverticulum of the gut-caeca. As in *Theletrum*, the uterine seminal receptacle tends to extend posteriorly to the vitellarium.

Family **DEROGENIDAE** Nicoll, 1910

Halipegidae Poche, 1926
Liocercidae Ejsmont, 1931

Body normally small; usually spindle-shaped to elongate oval. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed; ventral sucker usually near middle of body, occasionally more anterior or posterior. Pharynx well developed. Oesophagus short. 'Drüsenmagen' usually present. Gut-caeca end blindly or form cyclocoel. Testes two; symmetrical to tandem; pre- or post-ovarian; in hindbody. Seminal vesicle thin-walled; oval, elongate or tubular; not constricted into portions; in forebody; occasionally partly or wholly enclosed within sinus-sac. Pars prostatica usually tubular, occasionally vesicular; occasionally enclosed within sinus-sac. Ejaculatory duct short or absent; often within sinus-sac. Sinus-sac normally present, occasionally absent; usually small and oval; often weakly developed; may enclose all or part of pars prostatica and seminal vesicle. Permanent sinus-organ present as small cone or absent. Hermaphroditic duct normally present; occasionally absent; usually short. Genital atrium present or absent; usually small. Genital pore mid-ventral in forebody. Ovary oval; pre- or post-testicular. Mehlis' gland normally post-ovarian or occasionally at level of ovary. Seminal storage and disposal apparatus variable. Laurer's canal usually present; either opening dorsally to exterior or leading into Juel's organ; often dilated proximally to form small rudimentary seminal receptacle, which is occasionally enlarged to form an apparently functional canalicular seminal receptacle. Juel's organ absent or present in either rudimentary or fully-developed state. Blind seminal receptacle present rarely. Uterine seminal receptacle normally present; rarely absent. Uterus may or may not extend posterior to vitellarium; significant proportion of uterus usually coiled in forebody. Eggs numerous; with or without filaments or threads; rarely with anopercular spine. Vitellarium one or two masses; entire or lobed (lobes normally shallow, rarely digitate); pre- or post-ovarian; symmetrical, oblique or tandem. Excretory vesicle Y-shaped; arms united in forebody. Parasitic usually in gut (normally stomach) of freshwater and marine teleosts, but occasionally recorded from amphibians, reptiles and freshwater shrimps.

COMMENT. This is a family which does not have a constant seminal storage and disposal apparatus in the female system. As discussed below (p. 124), the variations of this apparatus probably occur because they are a diverse and successful, but relatively primitive group, which appear to have evolved at about the time when the first modifications of the primitive arrangement of the seminal storage and disposal apparatus began to occur. The variety of conditions found in this group tend to parallel those which have occurred during the evolution of some of the more advanced hemiuroids, such as the hemiurids, bunocotylids and lecithasterids.

Key to Derogenidae

1. A. Testes posterior to ovary and vitellarium . . . . . . **GONOCERCINAE** (p. 74)
   B. Testes anterior to ovary and vitellarium 2
2. A. Parasites primarily of freshwater teleosts, but occasionally present in brackish water or marine teleosts close to the ancient Sarmatic Sea region [Caspian, Black and Mediterranean Seas], in amphibians, in reptiles and in freshwater shrimps; ventral sucker occasionally anterior to middle of body; uterus not present posterior to vitellarium; sinus-sac, when present, may enclose part of or entire seminal vesicle and/or pars prostatica . . . . **HALIPEGINAE** (p. 75)
   B. Parasitic in marine teleosts; ventral sucker not present in anterior half of body; uterus often extends posterior to vitellarium; sinus-sac present, never enclosing any part of pars prostatica or seminal vesicle . . . . **DEROGENINAE** (p. 71)

Subfamily **DEROGENINAE** Nicoll, 1910

(?) Liopyginae Ejsmont, 1931
(?) Liocercinae Ejsmont, 1931
Genarchinae Skrjabin & Guschanskaja, 1955
Orthoruberinae Nasir & Gomez, 1977

Ventral sucker in middle or posterior to middle of body. Gut-caeca end blindly or form cyclocoel. Testes pre-ovarian; symmetrical to oblique. Seminal vesicle small; globular to tubular. Pars prostatica usually tubular, occasionally vesicular; short or long. Sinus-sac present; globular to cylindrical. Permanent sinus-organ present; small; cone-shaped. Hermaphroditic duct normally short. Genital atrium small; often filled by sinus-organ. Ovary close behind testes. Laurer's canal present or absent; opening dorsally or into rudimentary Juel's organ; may be dilated proximally forming large rudimentary or functional canalicular seminal receptacle. Blind seminal receptacle present when Laurer's canal and uterine seminal receptacle absent; latter usually present. Uterus coiled throughout hindbody and part of forebody; significant proportion of uterus often present posterior to vitellarium. Eggs without filaments or threads, but may have anopercular spine. Vitellarium two symmetrical to tandem, oval or slightly indented masses; posterior or occasionally lateral and postero-lateral to ovary. Parasitic in gut (mainly stomach) of marine teleosts.

Key to Derogeninae

1. A. Uterus not normally extending posterior to vitellarium 4
B. Significant proportion of uterus posterior to vitellarium 2
2. A. Cyclocoel present . . . . ***PROGONUS***
B. Gut-caeca end blindly 3
3. A. Eggs drawn into sharp point at anopercular pole . . . . ***DEROGENOIDES***
B. Eggs lacking point at anopercular pole . . . . ***DEROGENES***
4. A. Vitelline masses tandem to oblique, lateral and postero-lateral to ovary; blind seminal receptacle present . . . . ***LEURODERA***
B. Vitelline masses symmetrical to oblique, post-ovarian; Laurer's canal and presumably uterine seminal receptacle present . . . . ***GONOCERCELLA***

COMMENT. Initially, we considered *Gonocercella* and *Leurodera* to be members of the Halipeginae because of the pre-vitelline distribution of the uterus. The fact that they parasitize marine teleosts and the structure of the terminal genitalia, however, clearly associated them with the Derogeninae. It could also be argued that *Arnola*, *Magnibursatus* and *Tyrrhenia*, which are present in teleosts from the brackish to marine conditions of the Black and Mediterranean Seas, should be included in the Derogeninae. The structure of the terminal genitalia, however, is different from that of the latter group. In addition, these three genera are morphologically related to some of the Asian halipegines from freshwater and can be historically and zoogeographically related to the halipegines of the central Asian region via the ancient Sarmatic Sea.

DEROGENES Lühe, 1900 [n(w,s)]

(?) *Liopyge* Looss, 1899
(?) *Liocerca* Looss, 1902

Gut-caeca end blindly near posterior extremity. Testes symmetrical to oblique. Seminal vesicle globular to tubular and sinuous. Pars prostatica short to long. Sinus-sac globular. Male and female ducts unite within sinus-organ. Ovary usually close behind testes; may be lateral to posterior testis when latter is oblique. In *D. varicus* Laurer's canal opens distally into rudimentary Juel's organ and dilates proximally forming large rudimentary seminal receptacle. Uterine seminal receptacle present. Uterine field usually extends from posterior extremity to region of genital pore; significant proportion of uterus posterior to vitellarium. Eggs without anopercular spine. Vitelline masses symmetrical to oblique; globular or slightly indented; post-ovarian. Parasitic in stomach, oesophagus or occasionally gall-bladder of marine (? and freshwater) teleosts.

TYPE-SPECIES. *Derogenes ruber* Lühe, 1900 [by monotypy].

COMMENT. The overall morphology of *Liopyge bonnieri* (Monticelli, 1893) is probably identical to that of *Derogenes*, if the vitellarium and the testes have been confused. It is difficult to believe, however, that an experienced worker like Monticelli would make such a mistake, especially as he originally considered his specimens to be *Distoma varicum* [now *Derogenes varicus* (Müller, 1780)], and later re-named them *Distoma bonnieri*. Monticelli recorded this species from *Trigla* *gurnardus* in the English Channel. Evidence against the validity of the genus *Liopyge* is that in spite of the abundance of this host it has never been found a second time, although *Derogenes varicus* has been recorded from the English Channel in *Trigla gurnardus* by Nicoll (1914) and in *T. lucerna* by Nicoll (1914), Baylis & Jones (1933) and by ourselves: we have re-checked the determination of the last two records. Until there is more conclusive evidence for the existence of *Liopyge*, therefore, we are including this genus, and its synonym *Liocerca*, as questionable synonyms of *Derogenes*.

The genus *Pronopyge* Looss, 1899, has been considered to be a close relative of *Liopyge* (see Yamaguti, 1971). Its type-species was originally quoted as *P. ocreata* (Rudolphi, 1802); but *Fasciola ocreata* of Rudolphi (1802) was shown by Odhner (1911) to be a species of *Hemiurus*, and, as stated by Poche (1926), *Pronopyge* must be considered a junior synonym of the latter genus. Monticelli (1891) considered *Distoma ventricosum* Rudolphi, 1819 (and van Beneden, 1871) [*nec D. ventricosum* (Pallas, 1774)], and *Distomum carolinae* Stossich, 1889, to be synonyms of *Fasciola ocreata* Rudolphi, 1802. Figures of these two species by van Beneden (1871) and Stossich (1889) and of '*Apoblema ocreata*' by Monticelli (1891) suggest that they belong to the fellodistomid genus *Pseudopentagramma* Yamaguti, 1971 (a junior synonym of *Pronoprymna* Poche, 1926 – see Bray & Gibson, in prep.) and they are similar to figures of *Pseudopentagramma symmetrica* (Chulkova, 1939) produced by Margolis & Ching (1965).

DEROGENOIDES Nicoll, 1913

Gut-caeca end blindly. Testes symmetrical to oblique. Seminal vesicle small; globular. Pars prostatica short. Sinus-sac somewhat cylindrical with proximal end slightly enlarged. Sinus-organ (?) presumably present. Ovary immediately posterior to testes. Laurer's canal and Juel's organ (?). Seminal receptacle (? rudimentary) reported. Uterine seminal receptacle (?). Much of uterus present posterior to vitellarium. Eggs drawn out to sharp point at anopercular pole. Vitelline masses entire; symmetrical; post-ovarian. Parasitic in stomach and intestine of marine teleosts.

TYPE-SPECIES. *Derogenoides ovacutus* Nicoll, 1913 [by original designation].

COMMENT. *Derogenoides skrjabini* Vlasenko, 1931, was made the type-species of *Magnibursatus* by Naidenova (1969). *D. tetralecithum* Roman, 1955, and possibly *D. sargi* Pogoreltseva, 1954, also appear to be halipegines.

GONOCERCELLA Manter, 1940

Ventral sucker in posterior half of body. Gut-caeca end blindly. Testes oblique. Seminal vesicle tubular; coiled. Pars prostatica vesicular. Sinus-sac small. Sinus-organ a muscular cone. Ovary immediately posterior to testes; close to posterior extremity. Laurer's canal opens dorsally (according to MacCallum, 1913). Blind or canalicular seminal receptacle absent. Uterine seminal receptacle presumably present. Juel's organ presumably absent. Uterus mainly coiled in forebody; not reaching posterior to vitellarium. Eggs without anopercular spine. Vitelline masses entire; symmetrical; post-ovarian; close to posterior extremity. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Gonocercella pacifica* Manter, 1940 [by original designation].

LEURODERA Linton, 1910 [n(w)]

Orthoruberus Nasir & Gomez, 1977

Body oval; stout. Gut-caeca end blindly near posterior extremity. Testes symmetrical; largely or partly extra-caecal. Seminal vesicle tubular; slightly sinuous. Pars prostatica short; with few to many external gland-cells; may be partly tubular and vesicular anteriorly. Sinus-sac oval. Sinus-organ small (well developed and conical in *Orthoruberus*). Ovary just posterior to testes; close to posterior extremity. Laurer's canal, Juel's organ and uterine seminal receptacle apparently absent.

Blind seminal receptacle present; large; antero-ventral, antero-lateral or antero-dorsal to ovary. Uterus anterior to vitellarium; much of it pre-testicular. Eggs without anopercular spine. Vitelline masses entire or slightly indented; tandem to oblique; lateral and postero-lateral to ovary. Parasitic in gut (mainly stomach) of marine teleosts (especially Pomadasyidae).

TYPE-SPECIES. *Leurodera decora* Linton, 1910 [by original designation].

COMMENT. *Leurodera ocyri* Travassos, Teixeira de Freitas & Bührnheim, 1965, and *L. inaequalis* Travassos, Teixeira de Freitas & Bührnheim, 1966, are not, in our opinion, specimens of *Leurodera*. The descriptions appear to resemble *Lecithophyllum* and *Aponurus*, and Overstreet (1973) considered these two species to be synonyms of *Aponurus pyriformis* (Linton, 1910).

PROGONUS Looss, 1899 [t(w,s)]

Genarches Looss, 1902

Cyclocoel present. Testes symmetrical. Seminal vesicle elongate, spindle-shaped, elongate oval or globular. Pars prostatica short; slightly vesicular. Sinus-sac small; globular. Ovary sinistral; halfway between testes and posterior extremity. Canalicular seminal receptacle present. Laurer's canal ends blindly after passing dorsally through cyclocoel. Rudimentary Juel's organ present as small dilations of Laurer's canal at distal extremity and especially at junction with seminal receptacle. Uterine seminal receptacle absent. Uterus extends posteriorly to vitellarium; fills most of hindbody and some of forebody. Eggs without anopercular spine. Vitelline masses entire; symmetrical; post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Progonus muelleri* (Levinsen, 1881) [by original designation].

COMMENT. In agreement with Poche (1926) and Bray (in press), *Progonus* Looss, 1899, cannot be considered a junior homonym of *Progona* Berg, 1882 (Recommendation of Article 36, International Rules of Zoological Nomenclature, 1926; Article 56(a), International Code of Zoological Nomenclature, 1961).

The apparent canalicular seminal receptacle present in this genus is essentially a type of blind seminal receptacle, especially as Laurer's canal does not open dorsally. The canalicular seminal receptacle (*sensu stricto*) is not found in the Hemiuroidea, except in the case of *Trifoliovarium*, and is normally associated with the use of Laurer's canal as a vagina during copulation (see Gibson & Bray, 1975).

Subfamily **GONOCERCINAE** Skrjabin & Guschanskaja, 1955

Hemiperinae Yamaguti, 1958

Ventral sucker posterior to middle of body. Gut-caeca end blindly. Testes post-ovarian; tandem to symmetrical; near posterior extremity. Seminal vesicle usually small; oval to tubular; in forebody. Pars prostatica tubular; short; linked to seminal vesicle by short, aglandular duct. Sinus-sac absent or poorly developed. Sinus-organ absent or present as small, blunt cone. Hermaphroditic duct absent or short. Genital atrium small or apparently absent. Ovary between testes and vitellarium. Laurer's canal present; opening dorsally; dilated proximally forming small rudimentary seminal receptacle. Juel's organ absent. Uterine seminal receptacle present. Uterus entirely pre-ovarian; most of coils usually in forebody. Eggs filamented or not. Vitellarium two entire or indented, oval masses; symmetrical; antero- to postero-lateral to ovary. Parasitic in stomach or branchial cavity of marine teleosts.

Key to Gonocercinae

1. A. Eggs without filaments; sinus-sac and sinus-organ absent (but see comment on *Gonocerca*) *GONOCERCA*
   B. Eggs filamented; sinus-sac weakly developed; sinus-organ present. . . . *HEMIPERA*

GONOCERCA Manter, 1925 [t(w,s)]

Ventral sucker in posterior half of body. Testes tandem to almost symmetrical; at posterior extremity of body. Seminal vesicle small; thin-walled; oval; close behind genital pore. Pars prostatica short; tubular. Sinus-sac and sinus-organ absent [see Comment]. Hermaphroditic duct absent (assuming that the small cavity into which male and female ducts open is the genital atrium). Genital atrium small or apparently absent. Ovary median. Uterus entirely pre-ovarian; largely in forebody. Eggs without filaments. Vitelline masses lateral or antero-lateral to ovary; entire to indented. Parasitic in stomach of marine teleosts (especially in mid-ocean).

TYPE-SPECIES. *Gonocerca phycidis* Manter, 1925 [by monotypy].

COMMENT. Manter (1934) described *G. phycidis* and *G. crassa* with a genital papilla present in both, and Laurer's canal absent in the latter. Our sectioned material of *G. phycidis* indicates that a sinus-organ is absent and that a well-developed Laurer's canal is present (see Gibson, 1976: figs 14b and 14c).

Since Manter's work there have also been conflicting opinions as to the presence of Laurer's canal in *G. crassa*, Yamaguti (1938*b*) stating it to be present and Rees (1953) absent. Both Rees (1953) and Brinkmann (1975) agree that a small but distinct genital atrium and genital papilla (sinus-organ) are present in *G. crassa*. If this is so, this species can hardly be considered to be congeneric with the other species of the genus. In view of the great morphological variability of *G. phycidis* and the morphological similarity with *Derogenes varicus*, with which *G. crassa* has been recorded, we consider that any change in its taxonomic status should await a complete redescription.

HEMIPERA Nicoll, 1913 [t(w,s)]

Hemiperina Manter, 1934

Ventral sucker in posterior half of body. Testes symmetrical to oblique at posterior extremity. Seminal vesicle oval to tubular. Pars prostatica tubular; short. Seminal vesicle and pars prostatica may apparently be enclosed by common, sub-globular, parenchymatous capsule. Sinus-sac weakly developed; with diffuse musculature; enclosing base of sinus-organ and proximal region of genital atrium. Sinus-organ a blunt cone. Male and female ducts may open separately on sinus-organ or form short hermaphroditic duct. Ovary median. Uterus entirely pre-ovarian; largely in forebody. Eggs filamented. Vitelline masses antero- to postero-lateral to ovary; entire or slightly indented. Parasitic in stomach or branchial cavity of marine teleosts.

TYPE-SPECIES. *Hemipera ovocaudata* Nicoll, 1913 [by original designation].

Subfamily **HALIPEGINAE** Poche, 1926

Arnolinae Yamaguti, 1958
Monovitellinae Ataev, 1970

Ventral sucker usually near middle of body, occasionally more anterior or posterior. Gut-caeca end blindly or form cyclocoel. Testes pre-ovarian; symmetrical to oblique or occasionally tandem to oblique. Seminal vesicle globular to tubular; sometimes entirely or partly internal. Pars prostatica tubular to vesicular; normally short; sometimes internal. Sinus-sac present or absent; usually weakly developed; may enclose pars prostatica and all or part of seminal vesicle. Sinus-organ present or absent; when present usually small, poorly developed and cone-shaped. Hermaphroditic duct usually short, occasionally long; rarely absent. Genital atrium small. Ovary usually close to posterior extremity. Laurer's canal present; with dorsal pore or short and leading into Juel's organ. Rudimentary seminal receptacle often present when Laurer's canal opens dorsally. Blind or canalicular seminal receptacle absent. Uterine seminal receptacle present. Uterus entirely or almost entirely anterior to vitellarium; coils extend into forebody, except in cases with ventral sucker inside anterior half of body. Eggs with or without filaments or threads.

Vitellarium one or two masses at posterior extremity of body; usually entire, but sometimes with indistinct or digitate lobes. Excretory bifurcation normally in hindbody, occasionally in forebody. Usually parasitic in gut (normally stomach) of freshwater teleosts; also recorded from brackish water and marine teleosts close to the ancient Sarmatic Sea region (Caspian, Black and Mediterranean Seas), amphibians, reptiles and freshwater shrimps (the majority of genera occur in Asia).

COMMENT. Certain genera of halipegines are closely related, differing basically in the apparent presence or absence of filaments or threads on the eggs or in the degree of union between the two vitelline masses. One such group comprises *Allotangiopsis*, *Chenia*, *Genarchopsis*, *Monovitella* and *Tangiopsis*, all of which occur in central, southern and south-east Asia. Another such group is *Arnola*, *Magnibursatus* and possibly *Anguillotrema* and *Tyrrhenia*, which, with the exception of *Anguillotrema* from central China, come from the Black or Mediterranean Seas.

There appear to be fundamental differences in the seminal disposal apparatus in the female reproductive system, as some genera possess Laurer's canal with a dorsal opening and others have a fully developed Juel's organ. The systematic significance of this must await further work, because the arrangement in most of the genera is as yet unknown.

Key to Halipeginae

1.	A.	Eggs with filaments or threads	2
	B.	Eggs without filaments or threads	8
2.	A.	Cyclocoel present	3
	B.	Gut-caeca end blindly	4
3.	A.	Cyclocoel and excretory bifurcation in forebody	***ALLOTANGIOPSIS***
	B.	Cyclocoel and excretory bifurcation in hindbody	***GENARCHOPSIS***
4.	A.	Vitellarium a single mass	***CHENIA***
	B.	Vitellarium two similar masses	5
5.	A.	Vitelline masses entire; sinus-sac completely enclosing pars prostatica and seminal vesicle; ventral sucker in anterior half of body; uterine coils retained in hindbody	***MAGNIBURSATUS***
	B.	Vitelline masses usually lobed; ventral sucker near middle of body or more posterior; uterine coils extend into forebody	6
6.	A.	Vitelline masses lobed (usually with 4 and 5 small lobes) or occasionally entire	7
	B.	Vitelline masses with about 8 digitate extensions	***THOMETREMA***
7.	A.	Sinus-sac encloses pars prostatica and entire seminal vesicle; vitelline masses lobed	***ANGUILLOTREMA***
	B.	Sinus-sac usually weakly developed or (?) absent, sometimes enclosing prostatica gland-cells, occasionally enclosing pars prostatica, rarely enclosing distal extremity of seminal vesicle; vitelline masses usually lobed, occasionally entire	***HALIPEGUS***
8.	A.	Cyclocoel present; ventral sucker near middle of body; uterine coils extend into forebody	10
	B.	Gut-caeca end blindly	9
9.	A.	Ventral sucker in anterior half of body; uterine coils retained in hindbody	11
	B.	Ventral sucker near middle of body; uterine coils extend into forebody.	***TYRRHENIA***
10.	A.	Vitellarium a single mass	***MONOVITELLA***
	B.	Vitellarium two similar masses situated close together	***TANGIOPSIS***
11.	A.	Sinus-sac encloses pars prostatica and seminal vesicle	***ARNOLA***
	B.	Sinus-sac small, not enclosing pars prostatica and seminal vesicle.	***DEROPEGUS***

HALIPEGUS Looss, 1899 [t(w); n(w,s)]

Genarchella Travassos, Artigas & Pereira, 1928
Vitellotrema Guberlet, 1928
Dollfuschella Vercammen-Grandjean, 1960
Progenarchopsis Fischthal, 1976
Paravitellotrema Watson, 1976

Ventral sucker near middle of body. Gut-caeca end blindly. Testes symmetrical to slightly oblique. Seminal vesicle saccular. Pars prostatica short; often reduced. Sinus-sac usually weakly developed or (?) absent; often enclosing pars prostatica and, on some occasions, distal extremity of seminal vesicle. Temporary sinus-organ may be developed as conical papilla (may occasionally be permanent); on some occasions male and female ducts open separately through this papilla. Hermaphroditic duct, when present, short. Genital atrium normally small. Ovary usually separated from testes by uterus, but not always. Laurer's canal present, with dorsal pore; proximal region dilate forming rudimentary seminal receptacle. Juel's organ absent. Uterus not extending posteriorly to vitellarium; usually with about equal distribution in fore- and hindbodies. Eggs with long, single filament at anopercular pole. Vitellarium two relatively symmetrical masses; usually clearly four- and five-lobed, sometimes indistinctly lobed or entire. Parasitic in upper regions of gut (usually stomach) of freshwater teleosts, amphibians and reptiles; those from amphibians often recorded from mouth, one record from ear (Cosmopolitan).

Type-species. *Halipegus ovocaudatus* (Vulpian, 1859) [by monotypy].

Comment. Our concept of *Halipegus* may be considered wide; but, until more of the constituent species have been carefully and critically described, we believe that this concept is the most useful. In particular there appears to be a need for careful descriptions of the terminal genitalia in this genus: that of the type-species, for instance, is poorly known. The vitellarium is rather variable, the paired masses being distinctly lobed in the type-species and in most other species in the genus, weakly or indistinctly lobed in some species [e.g. *H. kessleri* (Grebnitzky, 1872)] and entire in some species [e.g. *H.* [=*Vitellotrema*] *fusipora* (Guberlet, 1928), *H.* [=*Genarchella*] *parva* (Travassos, Artigas & Pereira, 1928) and the two species of *Paravitellotrema* Watson, 1976]. *Halipegus cryptorchis* Mañe-Garzon & Gascon, 1973, is morphologically similar to *Deropegus*, especially in the rather anterior position of the ventral sucker. It differs, however, in the eggs being filamented and that part of the uterus is coiled in the forebody.

ALLOTANGIOPSIS Yamaguti, 1971

Ventral sucker in middle of body. Cyclocoel present in forebody. Testes symmetrical to oblique. Seminal vesicle tubular, stout, recurved. Pars prostatica short, tubular; not delimited. Sinus-sac forms muscular wall surrounding hermaphroditic duct (?). Sinus-organ absent (?). Laurer's canal and Juel's organ (?). Seminal receptacle reported [presumably either rudimentary type or Juel's organ]. Uterine seminal receptacle situated, at least partly, in distal region of uterus. Uterus not reaching posterior to vitellarium; significant proportion present in forebody. Eggs filamented. Vitellarium two lobed masses; slightly oblique; at posterior extremity. Excretory bifurcation in forebody. Parasitic in gonads of freshwater shrimps as (?) progenetic metacercaria (China).

Type-species. *Allotangiopsis shanghaiensis* (Yeh & Wu, 1955) [by original designation].

Comment. This genus is similar to *Tangiopsis*, differing only in the presence of filamented eggs and in the anterior positions of the cyclocoel and the excretory bifurcation. The latter differences might be explained by the relatively caudal position of the ventral sucker, a characteristic of metacercariae.

ANGUILLOTREMA Chin & Ku, 1974

Ventral sucker in posterior half of body. Gut-caeca end blindly. Testes symmetrical. Seminal vesicle tubular; coiled; internal. Pars prostatica vesicular; internal. Sinus-sac large; weakly muscled; enclosing pars prostatica and seminal vesicle. Sinus-organ muscular; conical. Laurer's canal and Juel's organ (?). Uterus entirely anterior to vitellarium; large proportion in forebody. Eggs with a filament at each end and small threads surrounding base of filament at one end. Vitellarium two masses with four and five lobes; symmetrical at posterior extremity. Parasitic in stomach of eels in freshwater (China).

Type-species. *Anguillotrema papillatum* Chin & Ku, 1974 [by original designation].

ARNOLA Strand, 1942 [t(w,s)]

Arnoldia Vlasenko, 1931, *nec* Mayer-Eymar, 1887

Ventral sucker in anterior half of body. Gut-caeca end blindly close to posterior extremity. Testes oblique; separated by uterus. Seminal vesicle coiled, tubular; internal. Pars prostatica short, straight; internal. Sinus-sac enclosing seminal vesicle and pars prostatica plus metraterm distally. Permanent sinus-organ absent. Short hermaphroditic duct and genital atrium present. Ovary immediately posterior to hind testis. Short, dilate Laurer's canal, containing sperm, opens into well-developed Juel's organ. Uterine seminal receptacle present. Uterus entirely anterior to vitellarium; coils not extending into forebody. Eggs without filaments. Vitellarium two symmetrical masses; situated close together at posterior extremity; slightly indented, usually indicating three and four lobes. Parasitic in stomach of marine teleosts (*Diplodus*) in Black Sea and Adriatic Sea.

Type-species. *Arnola microcirrus* (Vlasenko, 1931) [by original designation].

Comment. The low salinity of the Black Sea and the similarity between this genus and several genera from freshwater in Central Asia and the Far East suggest that *Arnola* might be a relict from the ancient Sarmatic Sea, which arose in the upper Miocene epoch, contained brackish water and extended from the Black Sea region easterly into Central Asia. Our finding *Arnola* in the Adriatic Sea in no way invalidates this hypothesis, as a connection between this region of the Mediterranean Sea and the Sarmatic Sea (then called the Karangat Sea) occurred briefly during the Pleistocene epoch [see Zenkevitch, 1947; Ekman, 1953; Miller, 1972].

This genus appears to be closely related to *Magnibursatus*, *Anguillotrema* and *Tyrrhenia*.

CHENIA Hsu, 1954

Ventral sucker just posterior to middle of body. Gut-caeca terminate blindly at level of ovary. Testes oblique. Seminal vesicle a curved, elongate sac. Pars prostatica internal (?; see figure 1 of Hsu). Sinus-sac enclosing attenuated anterior portion of seminal vesicle and pars prostatica. Sinus-organ not reported. (?) Seminal receptacle (presumably either rudimentary or Juel's organ) reported. Uterus entirely pre-ovarian; coils extending into forebody. Eggs reniform; with two filaments at one pole. Vitellarium single compact mass at posterior extremity. Parasitic in gut of freshwater gobiid teleosts (China).

Type-species. *Chenia cheni* Hsu, 1954 [by monotypy].

DEROPEGUS McCauley & Pratt, 1961

Parahalipegus Wootton & Powell, 1964

Ventral sucker in anterior half of body. Gut-caeca end blindly near posterior extremity. Testes tandem, oblique or symmetrical. Seminal vesicle saccular. Pars prostatica short; tubular to slightly vesicular; surrounded by dense layer of gland-cells. Sinus-sac apparently present, but weakly developed; small. Sinus-organ a muscular cone. Ovary usually separated from testes by loops of uterus. Laurer's canal present; apparently opening dorsally; slightly dilated proximally, forming a rudimentary seminal receptacle. Juel's organ presumably absent. Uterine coils not extending into forebody; one loop may reach posterior to vitellarium. Eggs without filaments. Vitellarium two symmetrical to oblique, entire or slightly lobed masses; close to posterior extremity. Parasitic in stomach of amphibians and teleosts in freshwater (North America).

Type-species. *Deropegus aspina* (Ingles, 1936) [by original designation].

GENARCHOPSIS Ozaki, 1925

Ophiocorchis Srivastava, 1933
(?) *Pseudogenarchopsis* Yamaguti, 1971

Ventral sucker in posterior half, or occasionally in middle, of body. Cyclocoel present in hindbody; oesophageal pouch often present. Testes usually oblique, occasionally symmetrical. Seminal vesicle tubular to elongate-saccular; coiled. Pars prostatica short; may be slightly vesicular. Sinus-sac not clearly described, but may be weakly developed and enclose pars prostatica and perhaps distal extremity of seminal vesicle. Sinus-organ a strongly muscular, blunt cone. Ovary usually sinistral and well posterior to testes. Laurer's canal opening into well-developed Juel's organ, or apparently opening dorsally (?). Uterus entirely pre-ovarian; coils extending into forebody. Eggs with long, polar filament. Vitellarium two entire or indented masses at posterior extremity; symmetrical to oblique. Parasitic mainly in stomach of freshwater teleosts, but there are two records from amphibians and two probable accidental infestations of snakes (Southern Asia and Far East).

TYPE-SPECIES. *Genarchopsis goppo* Ozaki, 1925 [by original designation].

COMMENT. *Genarchopsis thapari* Gupta & Chakrabarti, 1967, from the intestine of a snake, is known only from four immature worms, and it is probably a fish-parasite which has been ingested by the wrong host. Yamaguti (1971) erected the genus *Pseudogenarchopsis* for this species; but his only apparent valid criterion for doing so is that this species is purported to have a cirrus-sac. As far as *Ophiocorchis* is concerned, this genus is said to differ from *Genarchopsis* in possessing an oesophageal pouch. Rai (1972) found this feature either present or absent in one species (*G. goppo*), and it cannot be considered a character of generic importance.

A well-developed Juel's organ in *G. punctati* Agrawal, 1966, was described by Anjaneyulu (1967) and Madhavi & Rao (1974); but Ozaki (1925) described *G. goppo*, the type-species, as having Laurer's canal which opened dorsally. It seems unlikely that species with such apparently different seminal and vitelline disposal apparatus could be congeneric, but more detailed information is required on *G. goppo* and other species in this genus in order to resolve this problem. Both Rai (1972) and Pandey (1975) also note the presence of Laurer's canal in *G. goppo*, but neither of them states how it terminates.

MAGNIBURSATUS Naidenova, 1969

Ventral sucker in anterior half of body. Gut-caeca end blindly close to posterior extremity. Testes oblique, in anterior hindbody. Seminal vesicle coiled, tubular; internal. Pars prostatica short, straight; internal. Sinus-sac enclosing seminal vesicle and pars prostatica, plus the metraterm distally; in forebody. Sinus-organ absent. Short hermaphroditic duct or genital atrium present. Laurer's canal ends blindly (? in Juel's organ). Uterine seminal receptacle present. Ovary near posterior extremity; separated from testes by uterus. Uterus entirely anterior to vitellarium; coils not extending into forebody. Eggs with several (? six to eight) filaments (? threads) at each end. Vitellarium two oblique to symmetrical masses; close together at posterior extremity. Parasitic in stomach of euryhaline or marine teleosts (Black Sea region).

TYPE-SPECIES. *Magnibursatus skrjabini* (Vlasenko, 1931) [by original designation].

MONOVITELLA Ataev, 1970

Ventral sucker in middle of body. Cyclocoel present in hindbody. Testes symmetrical. Seminal vesicle saccular. Pars prostatica short; vesicular. Sinus-sac reported absent (figure suggests it might be present as weakly muscled, tubular jacket of hermaphroditic duct). Sinus-organ absent (?). Genital atrium short. Ovary lateral; apparently extra-caecal; situated between right testis and vitellarium. Laurer's canal and Juel's organ (?). Uterus almost entirely anterior to vitellarium, but descending loop reaches close to posterior extremity; coils extend into forebody. Eggs not filamented. Vitellarium a single, entire mass; lateral; apparently extra-caecal between ovary and posterior extremity. Parasitic in intestine of brackish water teleosts (Caspian Sea).

TYPE-SPECIES. *Monovitella cyclointestina* Ataev, 1970 [by original designation].

COMMENT. *Monovitella*, despite certain apparent differences, is remarkably similar to *Tangiopsis*, both of which are reported from gobiid fishes. Future work might show the two to be synonymous. *Chenia* is also morphologically similar and reported from gobiid fishes.

TANGIOPSIS Skrjabin & Guschanskaja, 1955

Ventral sucker in middle of body. Cyclocoel present; caeca unite anterior to testes. Testes symmetrical to oblique. Seminal vesicle tubular; recurved. Pars prostatica small; free in parenchyma (according to Tang, 1951; but his figure suggests that the prostatic glands may be delimited or that the duct is vesicular and he has omitted the external gland-cells). Sinus-sac apparently absent. Temporary sinus-organ may be present (?). Ovary between right testis and vitellarium. Laurer's canal opens dorsally. Juel's organ presumably absent. Rudimentary seminal receptacle apparently present. Uterus not passing posterior to vitellarium; almost entirely pre-ovarian; coils extend into forebody; apparently filled with spermatozoa throughout most of its length. Eggs without filaments. Vitellarium two slightly indented, symmetrical masses; close together at posterior extremity; united by short duct. Parasitic in stomach of freshwater teleosts (China).

TYPE-SPECIES. *Tangiopsis chinensis* (Tang, 1951) [by original designation].

COMMENT: This genus is similar to *Monovitella.*

THOMETREMA Amato, 1968

Ventral sucker in middle of body. Gut-caeca end blindly near posterior extremity. Testes oblique to symmetrical; separated by loops of uterus. Seminal vesicle tubular; stout; attenuated anteriorly; recurved. Pars prostatica with narrow lumen; surrounded by dense, oval mass of gland-cells. Sinus-sac not reported, but possibly present surrounding long hermaphroditic duct (see figures of Szidat, 1954). Sinus-organ present as small papilla in base of oval genital atrium (not reported by Amato, 1968). Ovary near posterior extremity; separated from testes by many loops of uterus; may have slightly irregular outline. Laurer's canal and Juel's organ (?). Uterus entirely pre-ovarian; coils extending into forebody. Eggs with one polar filament. Vitellarium two symmetrical masses of about eight short, digitate lobes, which are irregularly expanded distally. Parasitic in stomach of freshwater teleosts (*Plecostomus*), occasionally in estuarine conditions (South America).

TYPE-SPECIES. *Thometrema magnifica* (Szidat, 1954) n. comb. [syn. *T. portoalegrensis* Amato, 1968 – type by original designation].

COMMENT. This genus was erected for a new species, *T. portoalegrensis*, from *Plecostomus commersoni* in Brazil by Amato (1968). The species *Gonocercella magnifica* was described by Szidat (1954) from the same host in the estuary of the River Plate and from *Plecostomus plecostomus* in a neighbouring locality to Amato's record. Szidat's description is identical to that of Amato, with the exception that he described and figured the terminal genitalia in more detail and did not observe the filament on the egg. Considering that there is no evidence that Szidat teased out the eggs or sectioned his specimens, we have little hesitation in synonymizing the two species, as the presence of filamented eggs is often difficult to ascertain in whole-mounts.

*TYRRHENIA** Paggi & Orecchia, 1975

Ventral sucker near middle of body. Gut-caeca end blindly near posterior extremity. Testes oblique. Seminal vesicle saccular, but attenuated distally; internal. Pars prostatica (?) short, tubular (according to Paggi & Orecchia the prostatica cells empty into the hermaphroditic duct); internal. Sinus-sac enclosing entire seminal vesicle and pars prostatica, plus metraterm distally. Permanent sinus-organ absent. Hermaphroditic duct short. Genital atrium apparently absent (or small). Laurer's canal present, with rudimentary seminal receptacle. Juel's organ absent. Uterine seminal receptacle present. Ovary immediately posterior to hind testis. Uterine coils reach posteriorly to vitellarium and extend into forebody. Eggs without filaments. Vitellarium two entire, symmetrical masses; situated close together immediately posterior to ovary and close to posterior extremity. Parasitic in stomach and on gills of marine teleosts (*Blennius*) in Mediterranean (Tyrrhenian) Sea.

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* Paggi & Orecchia (1974) first used this name in an abstract, but without an accompanying description.

TYPE-SPECIES. *Tyrrhenia blennii* Paggi & Orecchia, 1975 [by original designation].

CHELATREMA Gupta & Kumari, 1970, *gen. inq.*
Genus of uncertain position

This genus was erected in an abstract by Gupta & Kumari (1970) for a new species, *C. smythi* [type by monotypy], from the Indian freshwater fish *Chela baccala.* It is said to belong to the subfamily Arnolinae of the family Hemiuridae. The genus is unrecognizable from the brief definition given, and appears to have characters unusual, or unknown, in the Hemiuroidea.

Family **DICTYSARCIDAE** Skrjabin & Guschanskaja, 1955

Cylindrorchiidae Poche, 1926
Aerobiotrematidae Yamaguti, 1958
Pelorohelminthidae Fischthal & Kuntz, 1964
Albulatrematidae Yamaguti, 1965
Tetrasteridae Oshmarin, 1965
Dollfustravassosiidae Teixeira de Freitas & Kohn, 1967

Body usually large; oval; stout or flattened. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed; ventral sucker in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' normally present (?). Gut-caeca end blindly close to posterior extremity. Testes two; large; symmetrical; oval or elongate; pre-ovarian; just posterior to ventral sucker. Seminal vesicle tubular; in forebody. Pars prostatica tubular. Sinus-sac well developed, poorly developed or absent. Permanent sinus-organ absent (? or present as small papilla); temporary sinus-organ may form. Genital atrium small or absent. Hermaphroditic duct well developed or indistinguishable from genital atrium; sometimes appears to be continuation of metraterm with ejaculatory duct entering laterally. Ovary oval or with four (or five) short or elongate lobes; normally separated from testes by loops of uterus. Juel's organ* and uterine seminal receptacle present. Laurer's canal and blind or canalicular seminal receptacle absent. Uterus almost entirely retained in hindbody; mainly pre-ovarian or with many loops in post-ovarian field. Eggs without filaments; may link together and form chains. Vitellarium with six to eight (usually seven, arranged three and four) oval to digitiform lobes, or with two lateral acinous groups of follicles or two compact multilobulate masses; postero- to antero-lateral or posterior to ovary. Excretory arms united in forebody. Parasitic in swim-bladder of physostomatous teleosts in a marine environment.

COMMENT: The almost unique niche of these parasites in the swim-bladder of physostomatous teleosts is shared in the Hemiuroidea by the genus *Isoparorchis.* Although considered to be closely related to the members of the Dictysarcidae by many authors, the latter genus differs because it occurs in a freshwater teleost and possesses several primitive features, such as Laurer's canal, a tubular vitellarium and a well-developed, muscular sinus-organ.

Key to Dictysarcidae

1. A. Uterus mainly pre-ovarian 2
B. Uterine field mainly post-ovarian . . CYLINDRORCHIINAE *subfam. inq.* (p. 83)

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* Observed in *Elongoparorchis* (see Madhavi & Rao, 1974) and *Dictysarca* (see Manter, 1947).

2. A. Ovary oval (entire or irregularly lobed); vitellarium two compact multilobulate masses or two acinous bunches of follicles; hermaphroditic duct indistinguishable from genital atrium . . . . **DICTYSARCINAE** (p. 82)
   B. Ovary 4– (or 5–) lobed; vitellarium 6–8 (usually 7) digitiform to oval lobes; hermaphroditic duct distinguishable from genital atrium. . . . . **ALBULATREMATINAE** (p. 82)

Subfamily **DICTYSARCINAE** Skrjabin & Guschanskaja, 1955

Body stout. Cuticular ridge may encircle mid-hindbody. Testes oval; entire or irregularly lobed. Sinus-sac and sinus-organ absent. Hermaphroditic duct indistinguishable from genital atrium; tubular; short. Ovary oval; entire or irregularly lobed; in posterior third of hindbody. Uterus mainly pre-ovarian, but some loops present in post-ovarian field. Vitellarium two compact multilobulate masses or two acinous bunches of follicles; antero- or postero-lateral to ovary. Usually parasitic in marine eels.

Key to Dictysarcinae

1. A. Cuticular ridge encircling mid-hindbody absent; ovary irregularly lobed; vitellarium in two, compact, multilobulate masses . . . . ***DICTYSARCA***
   B. Cuticular ridge encircling mid-hindbody present; ovary unlobed; vitellarium two groups of acinous follicles . . . . ***AEROBIOTREMA***

DICTYSARCA Linton, 1910

No cuticular ridge present encircling mid-hindbody. Testes irregularly lobed. Seminal vesicle sinuous. Pars prostatica well developed. Hermaphroditic duct appears to be continuation of metraterm, with ejaculatory duct entering laterally. Ovary large; irregularly lobed. Vitellarium two compact, multilobulate masses; antero-lateral to ovary. Parasitic in moray eels (*Gymnothorax*) and sea-horses (*Hippocampus*).

TYPE-SPECIES. *Dictysarca virens* Linton, 1910 [by original designation].

AEROBIOTREMA Yamaguti, 1958

Cuticular ridge present encircling mid-hindbody. Testes entire. Seminal vesicle sigmoid. Pars prostatica straight. Ovary small; entire. Vitellarium two acinous bunches of follicles; one antero- and one postero-lateral to ovary. Excretory arms with numerous anastomosing side branches, mostly lying close to caeca. Parasitic in marine eels (*Muraenesox*).

TYPE-SPECIES. *Aerobiotrema muraenesocis* Yamaguti, 1958 [by original designation].

Subfamily **ALBULATREMATINAE** Yamaguti, 1965

Pelorohelminthinae Fischthal & Kuntz, 1964
Tetrasterinae Oshmarin, 1965

Body flattened to stout. Testes large; oval or elongate. Sinus-sac present; well or poorly developed. Hermaphroditic duct distinguishable from genital atrium. Ovary four (or five) distinct, oval or elongate lobes; in middle or posterior half of hindbody. Uterus mainly pre-ovarian or extending throughout hindbody. Vitellarium seven (occasionally six or eight) digitiform to oval lobes; immediately posterior or postero-lateral to ovary. Parasitic in marine (? or brackish water) teleosts.

Key to Albulatrematinae

1. A. Vitelline lobes, ovarian lobes and testes oval; ovary in middle of hindbody; significant proportion of uterus post-ovarian. . . . . ***ALBULATREMA***

B. Vitelline lobes and ovarian lobes digitiform; testes elongate; ovary well inside posterior half of hindbody; most of uterus pre-ovarian . . . . ***ELONGOPARORCHIS***

ALBULATREMA Yamaguti, 1965

Body stout. Testes oval. Seminal vesicle tubular; narrow; convoluted [according to Yamaguti, 1965, the seminal vesicle is replaced by a vas deferens, the distal portion of which is strongly muscular, convoluted and enclosed by an apparently muscular capsule]. Pars prostatica sigmoid; delimited. Sinus-sac well developed; bulbous. Temporary sinus-organ may be present. Genital atrium absent or (?) small. Ovary in middle of hindbody; ovarian lobes oval. Uterus extends throughout hindbody, much of it post-ovarian. Vitelline lobes oval to pyriform. Parasitic in marine (? or brackish water) teleosts (*Albula*).

TYPE-SPECIES. *Albulatrema ovale* Yamaguti, 1965 [by original designation].

ELONGOPARORCHIS Rao, 1961 [n(w)]

Pelorohelmins Fischthal & Kuntz, 1964
Tetraster Oshmarin, 1965
Dollfustravassosius Teixeira de Freitas & Kohn, 1967

Body flattened to stout. Testes elongate. Seminal vesicle sinuous; may reach dorsally to ventral sucker. Pars prostatica short. Sinus-sac poorly developed; present only distally as vestige surrounding base of genital atrium. Sinus-organ a small papilla-like structure (? temporary). Hermaphroditic duct relatively long; formed as continuation of metraterm, with ejaculatory duct entering laterally. Genital atrium oval or elongate-oval. Ovary well inside posterior half of hindbody; ovarian lobes digitiform. Uterus mainly pre-ovarian. Eggs may be linked together forming chains. Vitelline lobes digitiform; with condensed follicular appearance. Parasitic especially in catfishes, such as *Arius*.

TYPE-SPECIES. *Elongoparorchis pneumatis* Rao, 1961 [by original designation].

COMMENT. In some descriptions of species of this genus Mehlis' gland has been considered to be the ovary and the ovary to be anterior lobes of the vitellarium (see Fischthal & Kuntz, 1964a; Teixeira de Freitas & Kohn, 1967; Fischthal & Thomas, 1968; but cf. Yamaguti, 1971).

Subfamily **CYLINDRORCHIINAE** Poche, 1926, *status emend.* (*subfam. inq.*)

[Original description inadequate.] Body elongate-oval. Testes elongate. Terminal genitalia not known. Ovary small; oval; just inside posterior half of hindbody. Uterus convoluted posterior to ovary; straight anterior to ovary. Vitellarium two clusters of small follicles; antero-lateral to ovary. Parasitic in marine (? or brackish water) teleosts (*Tetrodon*).

CYLINDRORCHIS Southwell, 1913, *gen. inq.*

Defined as subfamily.

TYPE-SPECIES. *Cylindrorchis tenuicutis* Southwell, 1913 [by original designation].

COMMENT. We have included *Cylindrorchis* as a *genus inquirendus* because the original description of *C. tenuicutis* is inadequate. Southwell (1913) states: 'As only very few specimens of this parasite were obtained, it was found impossible to satisfactorily make out with *certainty*, the precise details of the reproductive system. I am therefore not certain that the following description is absolutely correct in every detail'. If Southwell had confused the uterus with the vitellarium, the vitellarium for the ovary and the ovary for Mehlis' gland or Juel's organ, then it is conceivable that he may have been dealing with immature specimens of *Elongoparorchis*.

Theoretically, the oldest family-group name available in this family is Cylindrorchiidae Poche, 1926; but, due to the questionable validity of *Cylindrorchis*, we feel that it would be inadvisable, at this stage, to use this genus as the type-genus of the family.

Family **HEMIURIDAE** Looss, 1899

Lecithochiriidae Lühe, 1901
Dinuridae Looss, 1907
Elytrophallidae Skrjabin & Guschanskaja, 1954

Body usually small, but elongate. Ecsoma present, occasionally reduced or vestigial. Body-surface smooth or with annular plications; the latter occasionally being serrate giving a scaley appearance. Presomatic pit or ventro-cervical groove occasionally present. Oral and ventral suckers well developed; usually close together. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' normally present. Gut-caeca terminate blindly; usually within ecsoma. Testes two; tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular, saccular or constricted into portions; muscular or thin-walled; in fore- or hindbody. Pars prostatica of variable length; usually tubular, but occasionally vesicular; may be linked to seminal vesicle by aglandular duct. Ejaculatory duct, if present, usually short. Sinus-sac usually well developed, occasionally reduced or absent. Prostatic or ejaculatory vesicle occasionally present within sinus-sac. Hermaphroditic duct usually enclosed within sinus-sac. Permanent sinus-organ and genital atrium well developed, small or absent; temporary sinus-organ may form from hermaphroditic duct in some cases. Genital pore mid-ventral at level of oral sucker or pharynx. Ovary oval; usually entire; post-testicular. Mehlis' gland post-ovarian. Laurer's canal and canalicular or blind seminal receptacle absent. Juel's organ and uterine seminal receptacle present. Uterus coiled mainly in pre- and/or post-ovarian region of hindbody; few or no coils present in forebody; initially descending into or towards ecsoma and then ascending towards forebody. Eggs numerous; small; embryonated; rarely with a polar filament. Vitellarium varies between forms with seven tubular branches (three on one side of body, four on other) and forms with two distinct, oval masses; mainly post-ovarian. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic mainly in gut, especially stomach, of marine teleosts, occasionally present in gut of freshwater teleosts and lung of sea-snakes.

Key to Hemiuridae

1. A. Ejaculatory (or prostatic) vesicle present within sinus-sac, occasionally partly external [this vesicle should not be confused with a pars prostatic which is also present] . . 2
B. Ejaculatory (or prostatic) vesicle absent 4
2. A. Long, convoluted hermaphroditic duct and thin-walled permanent sinus-organ present; seminal vesicle bipartite, anterior part muscular; vitellarium 2 irregularly oval masses **GLOMERICIRRINAE** (p. 90)
B. Hermaphroditic duct relatively straight; permanent sinus-organ absent; seminal vesicle tubular or saccular and partitioned, usually thin-walled; vitellarium 7 digitiform to oval lobes or with tendency to form 2 distinct, often lobed, lateral masses; ecsoma sometimes reduced or apparently absent 3
3. A. Eggs with polar filament; commonly parasitic under surface of liver **HYPOHEPATICOLINAE** (p. 91)
B. Eggs without polar filaments; normally parasitic in gut . **LECITHOCHIRIINAE** (p. 91)
4. A. Sinus-sac absent or poorly developed, when present usually of 'open'-type; seminal vesicle entirely or mainly thin-walled, usually constricted into portions; ecsoma sometimes poorly developed. . . . . **PLERURINAE** (p. 95)
B. Sinus-sac present, usually well developed, occasionally small 5
5. A. Vitellarium 2 symmetrical to slightly oblique, entire or lobed masses 6
B. Vitellarium 7 distinct oval to tubular lobes 8
6. A. Seminal vesicle oval or bipartite, in fore- or hindbody; ecsoma well developed; parasitic in gut of marine teleosts 7
B. Seminal vesicle tubular, extending well into hindbody; ecsoma reduced; parasitic in lung of sea-snakes . . . . **PULMOVERMINAE** (p. 98)
7. A. Body-surface smooth; seminal vesicle in forebody, oval, thick-walled; sinus-sac very small **LETHADENINAE** (p. 95)
B. Body-surface with plications or 'scales'; seminal vesicle in hindbody, oval or bipartite, thin- or partly to entirely thick-walled . . . . . . **HEMIURINAE** (p. 85)

8.	A.	Seminal vesicle with thick muscular wall, oval; permanent sinus-organ normally delicate and amuscular	**ELYTROPHALLINAE** (p. 89)
	B.	Seminal vesicle thin-walled and oval, tubular or constricted into portions; permanent sinus-organ large and muscular, reduced to small papilla or apparently absent	**DINURINAE** (p. 86)

Subfamily **HEMIURINAE** Looss, 1899

Ecsoma well developed. Body-surface plicated or 'scaley' (i.e. with crenulate plications). Presomatic pit absent. Testes tandem to oblique. Seminal vesicle thin-walled, or partially or slightly muscular; bipartite or oval; in hindbody. Pars prostatica tubular; long; gland-cells occasionally delimited by membrane. Sinus-sac present; often tubular; not enclosing prostatic vesicle. Permanent sinus-organ absent, but hermaphroditic duct may be protruded to form temporary sinus-organ. Genital atrium usually small, but variable in length. Ovary oval. Vitellarium composed of two distinct oval masses, but these may show slight tendency toward lobation in three and four style. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

Key to Hemiurinae

1.	A.	Seminal vesicle bipartite	***HEMIURUS***
	B.	Seminal vesicle oval	2
2.	A.	Plications on body-surface normal	***PARAHEMIURUS***
	B.	Plications on body-surface crenulate, giving 'scaley' appearance	***ANAHEMIURUS***

HEMIURUS Rudolphi, 1809 [t(w,s); n(w, s)]

Apoblema Dujardin, 1845
Pronopyge Looss, 1899 (see p. 73).
Metahemiurus Skrjabin & Guschanskaja, 1954

Body-surface with normal plications. Seminal vesicle constricted into two portions (? occasionally three), one of which may have thick, muscular wall.

TYPE-SPECIES. *Hemiurus appendiculatus* (Rudolphi, 1802) [by subsequent designation: Stiles & Hassall, 1898].

COMMENT. Two subgeneric names have been erected: *Metahemiurus* Skrjabin & Guschanskaja, 1954, based upon sucker-ratios, the extent of the surface plications and the length of the ecsoma; and *Neohemiurus* Slusarski, 1958, based upon the presence of plications on the ecsoma. The former features are either variable or only of specific value, and the latter feature, plications on the ecsoma, is extremely doubtful (see p. 48) and requires confirmation. *Metahemiurus* has been used at the generic level by Brinkmann (1975).

ANAHEMIURUS Manter, 1947

Body-surface with 'scaley' appearance (i.e. with crenulate plications). Seminal vesicle oval; with relatively thick, muscular wall.

TYPE-SPECIES. *Anahemiurus microcercus* Manter, 1947 [by original designation].

PARAHEMIURUS Vaz & Pereira, 1930 [t(w)]

Body-surface with normal plications. Seminal vesicle oval; with muscular wall of variable thickness.

TYPE-SPECIES. *Parahemiurus merus* (Linton, 1910) [syn. *P. parahemiurus* Vaz & Pereira, 1930 – type by original designation].

Subfamily **DINURINAE** Looss, 1907

Stomachicolinae Yamaguti, 1958

Ecsoma well developed; occasionally large. Body surface plicated or smooth (apparently occasionally striated). Presomatic pit absent. Testes symmetrical to tandem; usually oblique. Seminal vesicle thin-walled; oval to tubular; may be constricted into two to four portions; in forebody, dorsal to ventral sucker or in hindbody. Pars prostatica tubular or vesicular; short or long; may be linked to seminal vesicle by aglandular duct. Sinus-sac present; small or large; usually oval; not enclosing a prostatic vesicle. Permanent sinus-organ large and muscular, reduced to small papilla or apparently absent. Genital atrium usually well developed; deep or shallow (often depending upon contraction). Ovary usually oval; occasionally reniform or lobed. Terminal portion of uterus may or may not form distinct vesicle just outside sinus-sac. Vitellarium normally seven tubular lobes; three on one side, four on the other. Excretory arms united or not united in forebody. Normally parasitic in stomach of marine teleosts.

Key to Dinurinae

1.	A.	Seminal vesicle usually (but not always) constricted into portions; permanent sinus-organ present, but occasionally reduced to small papilla (sectioning usually required); pars prostatica usually linked to seminal vesicle by distinct aglandular duct . . .	2
	B.	Seminal vesicle not constricted into portions; permanent sinus-organ usually apparently absent, but may be present as small papilla; pars prostatica not normally linked to seminal vesicle by distinct aglandular duct	7
2.	A.	Body-surface with plications	3
	B.	Body-surface without plications	4
3.	A.	Pars prostatica long, may be sparsely surrounded by gland-cells; seminal vesicle trilocular	***DINURUS***
	B.	Pars prostatica short, connected to seminal vesicle by long aglandular duct; seminal vesicle variable, tubular, saccular or divided into 2 or 3 sections . .	***ECTENURUS***
4.	A.	Glandular region of pars prostatica short; excretory arms unite in forebody; distal end of uterus often vesicular	5
	B.	Glandular region of pars prostatica long; distal end of uterus not vesicular . . .	6
5.	A.	Aglandular region of pars prostatica long; seminal vesicle dorsal or postero-dorsal to ventral sucker; sinus-sac usually dilate proximally	***ERILEPTURUS***
	B.	Aglandular region of pars prostatica short; seminal vesicle in forebody; sinus-sac elongate oval	***ATHERIA***
6.	A.	Parasitic in stomach of marine teleosts; pars prostatica connected to seminal vesicle by short aglandular duct; excretory arms not united in forebody . . .	***PARADINURUS***
	B.	Parasitic in intestine of freshwater teleosts	(?) ***PROSTERRHURUS***
7.	A.	Anterior part of hindbody greatly attenuated; pars prostatica in two parts separated by long aglandular duct	***MECODERUS***
	B.	Anterior part of hindbody with normal configuration; pars prostatica undivided . .	8
8.	A.	Ecsoma large; seminal vesicle oval or elongate-oval	9
	B.	Ecsoma normal; seminal vesicle tubular and sinuous	***TUBULOVESICULA***
9.	A.	Seminal vesicle in forebody	***ALLOSTOMACHICOLA***
	B.	Seminal vesicle in hindbody	***STOMACHICOLA***

COMMENT. We considered separating this group into two, using the features in the first part of the key, because of the functional association between the presence of a permanent sinus-organ and a seminal vesicle constricted into sections by sphincter muscles (see p. 129). The two groups, however, appear to grade into one another.

DINURUS Looss, 1907 [n(w,s)]

Body-surface with plications. Seminal vesicle trilocular, or occasionally quadrilocular; in anterior hindbody or occasionally postero-dorsal to ventral sucker. Pars prostatica long; may be densely or sparsely invested by gland-cells; linked to seminal vesicle by aglandular duct. Sinus-sac and permanent sinus-organ present; of variable size. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Dinurus tornatus* (Rudolphi, 1819) [by original designation].

ALLOSTOMACHICOLA Yamaguti, 1958

Ecsoma enormous. Body-surface smooth. Seminal vesicle elongate-oval; in forebody. Pars prostatica short; vesicular [? or long, tubular; see fig. 13b of Chauhan, 1954]; not connected to seminal vesicle by distinct aglandular duct. Sinus-sac present; small; oval. Permanent sinus-organ apparently absent. Ovary reniform; may be indistinctly lobed. Majority of uterus within ecsoma; normally fills more than half of ecsoma. Excretory arms (?) united in forebody.

TYPE-SPECIES. *Allostomachicola secundus* (Srivastava, 1937) [by original designation].

COMMENT. *Stomachicola lepturusi* Gupta & Gupta, 1976, appears to belong to this genus.

ATHERIA Hafeezullah, 1975

Body-surface smooth. Seminal vesicle saccular; in forebody. Pars prostatica short, tubular; connected to seminal vesicle by short, aglandular duct. Sinus-sac present; elongate-oval. Permanent sinus-organ present; (?) long, muscular. Ovary oval. Distal extremity of uterus vesicular. Excretory arms united in forebody.

TYPE-SPECIES. *Atheria zakiae* Hafeezullah, 1975 [by original designation].

COMMENT. This genus is apparently close to *Erilepturus* as a terminal dilation of the uterus occurs in both genera, although it has not been reported in all species of *Erilepturus*. The differences in the shape of the sinus-sac and in the length of the aglandular part of the pars prostatica are of questionable generic importance in this case; but we provisionally accept this genus on the basis of the distinct difference in the position of the seminal vesicle.

ECTENURUS Looss, 1907 [t(w); n(w)]

Magnacetabulum Yamaguti, 1934
Parectenurus Manter, 1947

Body-surface with plications. Seminal vesicle saccular, tubular or divided into two or three sections; postero-dorsal to ventral sucker or in anterior hindbody. Pars prostatica short (? or missing); connected to seminal vesicle by long, aglandular duct. Sinus-sac and permanent sinus-organ present; small. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Ectenurus lepidus* Looss, 1907 [by original designation].

ERILEPTURUS Woolcock, 1935 [n(w)]

Uterovesiculurus Skrjabin & Guschanskaja, 1954

Body-surface smooth (or finely transversely striated). Seminal vesicle variable; (?) oval, tubular to trilocular in the same species; dorsal or postero-dorsal to ventral sucker. Pars prostatica short, tubular; connected to seminal vesicle by long, aglandular duct. Sinus-sac present; dilate proximally (? or tubular). Permanent sinus-organ present; small. Ovary oval. Distal extremity of uterus (outside sinus-sac) may be vesicular. Excretory arms united in forebody.

TYPE-SPECIES. *Erilepturus tiegsi* Woolcock, 1935 [by original designation].

COMMENT. The vesicular nature of the terminal portion of the uterus, used by Skrjabin & Guschanskaja (1954) to erect *Uterovesiculurus*, is also found in *Erilepturus platycephali* (Yamaguti, 1934) according to Manter (1970), and possibly in other species of this genus. It is not clear whether this is a transient feature. In some species, such as those described by Yamaguti (1970), the proximal dilation of the sinus-sac is apparently missing.

MECODERUS Manter, 1940

Anterior part of hindbody attenuated. Body-surface smooth. Seminal vesicle saccular; well back in hindbody, just anterior to testes. Pars prostatica in two parts, one anterior to and other posterior to attenuated part of body, connected by long, aglandular duct; not connected to seminal vesicle by distinct aglandular duct. Sinus-sac present; small, oval. Permanent sinus-organ apparently absent. Ovary oval. Excretory arms united in forebody.

TYPE-SPECIES. *Mecoderus oligoplitis* Manter, 1940 [by original designation].

COMMENT. There are certain morphological similarities between this genus and *Stomachicola magna* (Manter, 1931).

PARADINURUS Vigueras, 1958 [t(w,s)]

Body-surface smooth. Seminal vesicle trilocular; at level of ventral sucker. Pars prostatica tubular; long; densely invested with gland-cells; connected to seminal vesicle by short, aglandular duct. Sinus-sac oval; thick-walled; relatively large. Permanent sinus-organ well developed. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Paradinurus manteri* Vigueras, 1958 [by original designation].

(?) *PROSTERRHURUS* Fischthal & Kuntz, 1963

Body-surface smooth. Seminal vesicle trilocular; in hindbody. Pars prostatica long, tubular; densely surrounded by gland-cells; apparently not linked to seminal vesicle by distinct, aglandular duct. Sinus-sac short; tubular. Permanent sinus-organ present; small. Ovary oval. Excretory arms (?). Parasitic in intestine of freshwater teleosts (? from estuarine region).

TYPE-SPECIES. *Prosterrhurus labeonis* Fischthal & Kuntz, 1963 [by monotypy].

COMMENT. The validity of this genus, which is based upon a single specimen, is questionable, because of shortcomings in its description and affinities with *Erilepturus*. The details of the terminal genital apparatus are based upon figure 687 of Yamaguti (1971). According to Fischthal & Kuntz (1963), there is an elongate sinus-sac which encloses the distal ends of the pars prostatica plus the metraterm, a prostatic vesicle, an ejaculatory duct and the hermaphroditic duct.

STOMACHICOLA Yamaguti, 1934

Pseudostomachicola Skrjabin & Guschanskaja, 1954
Acerointestinecola Jahan, 1970
Indostomachicola Gupta & Sharma, 1973

Ecsoma enormous. Body-surface smooth. Seminal vesicle oval; in hindbody. Pars prostatica tubular; long; sinuous; not connected to seminal vesicle by distinct aglandular duct; external gland-cells may not be evenly distributed throughout length. Sinus-sac present; small; oval. Permanent sinus-organ absent or reduced to rudiment. Ovary oval to reniform. Majority of uterine coils within ecsoma; normally fill less than half of ecsoma. Excretory arms united in forebody.

TYPE-SPECIES. *Stomachicola muraenesocis* Yamaguti, 1934 [by original designation].

TUBULOVESICULA Yamaguti, 1934 [n(s)]

Lecithurus Pigulewsky, 1938

Body-surface smooth. Seminal vesicle tubular; sinuous; in hindbody. Pars prostatica with long, wide lumen; sinuous or straight; not connected to seminal vesicle by distinct aglandular duct. Sinus-sac present; oval. Permanent sinus-organ normally absent, but may occur as small papilla.

Ovary oval to round. Vitelline lobes tubular, but often stout. Excretory arms united in forebody. Parasitic in stomach, body-cavity and body-tissues of marine teleosts (also reported from intestine of sea-snake).

TYPE-SPECIES. *Tubulovesicula spari* Yamaguti, 1934 [by original designation].

COMMENT. See Sinclair *et al.* (1972) and Stunkard (1973) concerning *Tubulovesicula* v. *Stomachicola*. Several authors, such as Sogandares-Bernal (1959), consider *T. lindbergi* (Layman, 1930) to be a senior synonym of the type-species of this genus.

Subfamily **ELYTROPHALLINAE** Skrjabin & Guschanskaja, 1954

Musculovesiculinae Skrjabin & Guschanskaja, 1954

Ecsoma well developed. Body-surface smooth or plicated. Pre-somatic pit absent, but ventro-cervical groove often present. Testes tandem to symmetrical, usually oblique. Seminal vesicle with exceptionally thick, muscular wall; oval, not constricted into portions; present in forebody, dorsal to ventral sucker or in hindbody. Pars prostatica tubular; long or short; usually linked to seminal vesicle by short, aglandular duct. Sinus-sac present; commonly tubular, long; not enclosing ejaculatory or prostatic vesicle. Sinus-organ usually well developed, but delicate and amuscular. Genital atrium usually deep (depending upon contraction). Ovary oval. Eggs rarely filamented. Vitellarium seven tubular to tear-shaped lobes, three on one side, four on the other, which may form rosette. Excretory arms united in forebody. Parasitic mainly in stomach of marine teleosts.

Key to Elytrophallinae

1. A. Body-surface with plications 2
   B. Body-surface without plications 4
2. A. Glandular region of pars prostatica mainly in hindbody 3
   B. Glandular region of pars prostatica in forebody . . . . . . *CLUPENURUS*
3. A. Sinus-sac long and narrow, reaching to the level of the seminal vesicle; vitelline lobes tear-shaped. . . . . *ELYTROPHALLOIDES*
   B. Sinus-sac relatively long, but not reaching to level of seminal vesicle; vitelline lobes tubular . . . . *LECITHOCLADIUM*
4. A. Seminal vesicle in forebody; eggs may be filamented . . . . *MUSCULOVESICULA*
   B. Seminal vesicle in hindbody; eggs not filamented . . . . . *ELYTROPHALLUS**

ELYTROPHALLUS Manter, 1940

Body-surface smooth. Seminal vesicle small to large; in hindbody. Pars prostatica sinuous; mainly or entirely in hindbody. Sinus-sac long, tubular, thick-walled. Vitelline lobes tear-shaped to digitiform. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Elytrophallus mexicanus* Manter, 1940 [by original designation].

(?) *CLUPENURUS* Srivastava, 1935

Body-surface with plications. Testes symmetrical to oblique. Seminal vesicle compact, oval; in hindbody. Pars prostatica in forebody. Sinus-sac bulbous; small. Vitelline lobes tubular. Parasitic in stomach of migratory clupeid teleosts (in freshwater).

TYPE-SPECIES. *Clupenurus piscicola* Srivastava, 1935 [by original designation].

COMMENT. The taxonomy of the hemiurid parasites of *Hilsa* (=*Clupea*; =*Ilisha*) *ilisha* is confused, as the descriptions of the species recorded either contain questionable features or are totally inadequate. In addition to *Clupenurus piscicola*, the following species of hemiurid have been recorded from this host:

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* *Johniophyllum* is inadequately described, but keys to this position.

Lecithocladium ilishae Mamaev, 1970, *nec* Bashirullah & D'Silva, 1973.
Lecithocladium ilishae Bashirullah & D'Silva, 1973, *nec* Mamaev, 1970.
Lecithocladium chauhani Hafeezullah, 1975.

Some of these descriptions indicate relationships with the elytrophallines and others with the dinurines; but the problem cannot be resolved until a comparative study of these forms, some of which are probably synonymous, is undertaken.

ELYTROPHALLOIDES Szidat, 1955 [T(w,s); t(w,s)]

Body-surface with plications. Seminal vesicle large, reaching back to level of testes. Pars prostatica sinuous; in hindbody. Sinus-sac long, normally reaching back to level of seminal vesicle. Vitelline lobes tear-shaped. Parasitic in stomach of marine teleosts (in southern hemisphere).

TYPE-SPECIES. *Elytrophalloides oatesi* (Leiper & Atkinson, 1914) [syn. *E. merluccii* Szidat, 1955 – type by original designation].

(?) *JOHNIOPHYLLUM* Skrjabin & Guschanskaja, 1954

[Inadequately described.] Body-surface smooth. Seminal vesicle small; in hindbody. Details of sinus-sac and pars prostatica not known. Vitelline lobes digitiform. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Johniophyllum johnii* (Yamaguti, 1938) [by original designation].

LECITHOCLADIUM Lühe, 1901 [t(w); n(w,s)]

Body-surface with plications. Oral sucker often funnel-shaped. Pharynx elongate. Seminal vesicle large; in hindbody. Pars prostatica long and sinuous; mainly or entirely in hindbody. Sinus-sac tubular; narrow; not reaching level of seminal vesicle and usually entirely or mainly in forebody. Vitelline lobes long and tubular. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Lecithocladium excisum* (Rudolphi, 1819) [by original designation].

MUSCULOVESICULA Yamaguti, 1940

Body-surface smooth. Seminal vesicle elongate; in forebody or overlapping ventral sucker. Pars prostatica short and indistinct; in forebody. Sinus-sac elliptical to pyriform; short. Vitelline lobes digitiform. Eggs may be filamented. Parasitic in stomach of marine teleosts (eels).

TYPE-SPECIES. *Musculovesicula gymnothoracis* Yamaguti, 1940 [by original designation].

Subfamily **GLOMERICIRRINAE** Yamaguti, 1958

Ecsoma well developed. Body-surface plicated. Pre-somatic pit absent. Testes oblique to tandem. Seminal vesicle bipartite; both parts globular to spindle-shaped; anterior part muscular; in hindbody or dorsal to ventral sucker. Pars prostatica tubular; short; linked to seminal vesicle by aglandular duct. Claviform sinus-sac present; in fore- or reaching into hindbody; enclosing prostatic vesicle. Hermaphroditic duct convoluted. Sinus-organ present; amuscular; long; convoluted. Genital atrium well developed. Vitellarium two irregularly oval, symmetrical masses. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

GLOMERICIRRUS Yamaguti, 1937 [n(w,s)]

Defined as subfamily.

TYPE-SPECIES. *Glomericirrus amadai* Yamaguti, 1937 [by original designation].

COMMENT. The interpretation of the terminal genitalia, based on our own sectioned material, differs markedly from the early descriptions (Yamaguti, 1937, 1938b). The observations of Manter (1970) and Campbell & Munroe (1977) agree with our interpretation.

Subfamily **HYPOHEPATICOLINAE** Skrjabin & Guschanskaja, 1954

Body spindle-shaped. Ecsoma reduced; appears to be permanently withdrawn. Body-surface smooth. Presomatic pit absent. Gut-caeca end blindly. Testes symmetrical at level of middle or posterior margin of ventral sucker. Seminal vesicle anterior or antero-dorsal to ventral sucker; constricted into two portions; elongate saccular; may be sinuous. Pars prostatica short; slightly vesicular; may be linked to seminal vesicle by short, aglandular duct. Sinus-sac present; oval; enclosing prostatic vesicle, part of metraterm and hermaphroditic duct. Permanent sinus-organ absent. Genital atrium present. Ovary oval. Much of uterus post-ovarian. Eggs with long, polar filament. Vitellarium seven digitiform lobes (three on one side, four on the other), forming post-ovarian rosette. Excretory arms united in forebody. Parasitic under connective tissue membrane of liver and in gut of marine teleosts.

HYPOHEPATICOLA Yamaguti, 1934 [t(w)]

Defined as subfamily.

TYPE-SPECIES. *Hypohepaticola callionymi* Yamaguti, 1934 [by original designation].

COMMENT. This representative of a monospecific subfamily was originally found under the connective tissue membrane of the liver, a very unusual habitat: it has also been recorded by Yamaguti (1942) from the stomach of the type-host, *Callionymus valenciennesi*, and from the intestine of *Monacanthus cirrhifer*. Yamaguti states, 'The proper location of the worm may be the stomach of *C. valenciennesi* as is the case with one of the present examples, but in fact it occurs more frequently on the surface of the liver. *M. cirrhifer* may be an accidental host.' We have examined material from the liver of *M. cirrhifer* collected by Dr A. Ichihara from Sagami Bay, Japan, in 1966, and specimens were recorded from the liver of *Callionymus flagris* by Ichihara *et al.* (1963), so it appears that the liver is the normal site of this parasite.

In our conception of *Hypohepaticola*, we have interpreted Yamaguti's (1934) 'distal portion of the pars prostatica' as being a prostatic vesicle and his 'small receptaculum seminalis' as being Juel's organ. In our view this genus is morphologically similar to the Lecithochiriinae, differing fundamentally according to the original description, only in the apparent absence of an ecsoma and the presence of filamented eggs. These two features are probably associated with the peculiar site of this parasite, as the presence of an ecsoma would not be significantly advantageous under the surface-membrane of the liver, whilst the presence of filaments on the eggs may aid their evacuation from the tissues of the host.

When we examined specimens from *M. cirrhifer* we could with some difficulty distinguish a withdrawn ecsoma. There is no evidence that this small structure is ever extruded. This suggests that *Hypohepaticola* is closely related to the Lecithochiriinae, especially as there is a tendency for the reduction of the ecsoma to occur in the latter group. For the present, however, we have retained the subfamily Hypohepaticolinae, because of the unusual habitat and the filamented eggs.

Hypohepaticola andamanensis Gupta & Miglani, 1974, from 'a teleost marine fish' off India, appears, from the brief description given, to possess none of the definitive characters of this genus. Their later (1976) description suggests that it is a lecithasterid.

Subfamily **LECITHOCHIRIINAE** Lühe, 1901

Sterrhurinae Looss, 1907
Brachyphallinae Skrjabin & Guschanskaja, 1955
Trithelaminae Yeh, 1955
Tricotyledoniinae Skrjabin & Guschanskaja, 1957
Dissosaccinae Yamaguti, 1958

Ecsoma usually well developed, occasionally reduced. Body-surface usually smooth, but occasionally plicated or rugate. Muscular 'shoulder-pads' present or absent. Presomatic pit and ventro-cervical groove present or absent. Testes tandem to symmetrical, usually oblique. Seminal vesicle elongate; constricted into two portions, which are occasionally separated by a duct, or tubular and convoluted; in bipartite forms anterior half may have thicker wall; normally in forebody, but forms with halves separated by duct may extend into hindbody. Pars prostatica short; vesicular or tubular; may extend slightly into base of sinus-sac; linked to seminal vesicle by short, aglandular duct. Sinus-sac present; rarely of 'open'-type; enclosing distinct ejaculatory or prostatic vesicle and metraterm. Permanent sinus-organ absent. Genital atrium usually small or absent, occasionally well developed. Ovary oval. Uterus mainly pre-ovarian or roughly equally distributed in pre- and post-ovarian fields. Eggs without filaments. Vitellarium seven digitiform to oval lobes in lateral groups of three and four, or with tendency to become two distinct lateral masses which often exhibit three and four lobes. Excretory arms united in forebody. Normally parasitic in gut of marine teleosts.

COMMENT. It is important to distinguish a prostatic (or ejaculatory) vesicle from a vesicular pars prostatica, otherwise difficulties of distinguishing some lecithochiriine and plerurine species become apparent. A prostatic (or ejaculatory) vesicle occurs entirely or mostly within a sinus-sac and together with a typical (external) pars prostatica from which it can be differentiated. In some plerurine genera which possess a recognizable sinus-sac, e.g. *Synaptobothrium*, the pars prostatica extends into the base of the 'open' sinus-sac, but the region of the pars prostatica inside the sinus-sac is indistinguishable from the region outside.

One could possibly divide the Lecithochiriinae into two groups: (1) those with a distinctly seven-lobed vitellarium; and (2) those with a vitellarium composed of two entire or indistinctly lobed masses. We feel that the two groups do grade into one another, as the lobation in some species of *Lecithochirium* is reduced, whilst three- and four-lobed vitelline masses can be seen in some specimens of *Brachyphallus*. Some caution, therefore, should be exercised when using the key presented below.

Key to Lecithochiriinae

1.	A.	Vitellarium 7 distinct oval to digitiform lobes	2
	B.	Vitellarium 2 entire masses which may be indistinctly 3- and 4-lobed	6
2.	A.	Large, muscular 'shoulder-pads' present	3
	B.	Large, muscular 'shoulder-pads' absent	4
3.	A.	Small accessory sucker present anterior to oral sucker	***TRICOTYLEDONIA***
	B.	No small accessory sucker	***CYATHOLECITHOCHIRIUM***
4.	A.	Small muscular pad present anterior to oral sucker	***CATARINATREMA***
	B.	Pre-oral lobe only present anterior to oral sucker	5
5.	A.	Large, eversible genital atrium present	***PLICATRIUM***
	B.	Normal small genital atrium present	***LECITHOCHIRIUM***
6.	A.	Seminal vesicle composed of two parts separated by narrow duct and reaches into hindbody	7
	B.	Seminal vesicle in forebody, tubular or bipartite, parts not separated by a duct.	8
7.	A.	Body-surface plicated anteriorly	***PSEUDODINOSOMA***
	B.	Body-surface smooth	***DISSOSACCUS***
8.	A.	Seminal vesicle bipartite; body-surface plicated; deep presomatic pit present	***BRACHYPHALLUS***
	B.	Seminal vesicle a wide, convoluted tube; body-surface smooth; presomatic pit absent; ecsoma reduced	***PROLECITHOCHIRIUM***

LECITHOCHIRIUM Lühe, 1901 [t(w,s); n(w,s)]

Sterrhurus Looss, 1907
Ceratotrema Jones, 1933
Jajonetta Jones, 1933
Separogermiductus Skrjabin & Guschanskaja, 1955

Magniscyphus Reid, Coil & Kuntz, 1965
Neohysterolecitha Ahmad, 1977

Ecsoma well or poorly developed. Body-surface smooth. Pre-oral lobe rarely with two lateral knobs. Presomatic pit and/or ventro-cervical groove often present. Seminal vesicle bipartite, tripartite or occasionally coiled; in forebody. Pars prostatica tubular, with wide lumen, to vesicular. Short, narrow extension of pars prostatica and/or ejaculatory duct may be present within sinus-sac. Ejaculatory (or prostatic) vesicle linked posteriorly to antero-dorsally with pars prostatica or ejaculatory duct. Temporary sinus-organ may form. Vitellarium two lateral masses; usually divided into three and four oval to digitiform lobes. Parasitic in gut (mainly stomach) of marine teleosts; also recorded from body-cavity, hepatic ducts and gills of marine teleosts and (?) gut of freshwater reptiles.

TYPE-SPECIES. *Lecithochirium rufoviride* (Rudolphi, 1819) [by original designation].

COMMENT. *Sterrhurus* is supposed to be distinguished from *Lecithochirium* by the absence of a presomatic pit (Lloyd, 1938; Manter & Pritchard, 1960a). The systematic significance of the presomatic pit has been discussed by Jones (1943) and Nasir & Diaz (1971). It appears to us that observations of this character have, in the past, not been careful enough. Many authors appear to have mistaken the ventro-cervical groove, which occurs commonly in this genus, for a presomatic pit, with the result that some descriptions must remain questionable. For example, Nahhas & Short (1965) described specimens of *Lecithochirium mesosaccum* Manter, 1947, from *Sciaenops ocellata* with a presomatic pit and from *Synodus foetans* without. If this character is to be taken as distinguishing these two genera, it would appear that specimens from *Sciaenops* are not representative of the same genus as those from *Synodus*. If we assume that Nahhas & Short mistook the ventro-cervical groove, a structure with a transitory nature, for a presomatic pit which is a permanent structure (see p. 49), then the specimens can be considered synonymous. We have examined the type-species of *Lecithochirium* and can confirm that a small [compared with that of *Brachyphallus* and *Synaptobothrium*] presomatic pit is present. This is visible in sections, but barely so in whole-mounts. We can also confirm that this structure is absent in *Lecithochirium musculus* (Looss, 1907), the type-species of *Sterrhurus*. Considering its small size in *L. rufoviride* and the questionable value of some of the information in the literature, we consider it to be inadvisable at present to distinguish these two genera on this feature, although future work, involving the examination of many species in *transverse sections*, might show that it is a valid taxonomic criterion.

Another feature used to distinguish *Lecithochirium* from *Sterrhurus* is the presence of a prostatic vesicle in the former and an ejaculatory vesicle in the latter (Crowcroft, 1946). The difference between these two types of vesicle is the presence of a lining of gland-cells in the case of the prostatic vesicle [we prefer to call the latter a glandular ejaculatory vesicle]. It appears, however, that these gland-cells can be lost, their concentration in one species varies and that they may in fact be present or absent in the same species (Manter & Pritchard, 1960a; Nasir & Diaz, 1971). This feature, therefore, appears to be of little value, except as an aid to specific identification. Contrary to the work of other authors, e.g. Jones (1943), in our sectioned material of *L. rufoviride* there are no gland-cells lining the ejaculatory vesicle; but, as in the case of *L. musculus*, the distal ends of some of the cells lining the pars prostatica do extend into the proximal extremity of the vesicle.

Separogermiductus was distinguished from *Lecithochirium* in having 'a bulbous ejaculatory vesicle, almost as large or even larger than the pharynx, lined with a refractive non-cellular wall, empty of cells or droplets, and into which the pars prostatica enters dorsally and anteriorly' (Manter & Pritchard, 1960a). We have had the opportunity of examining specimens of *Lecithochirium genypteri* Manter, 1954, which is considered by Manter & Pritchard (1960a) to be a species of *Separogermiductus*. The terminal genitalia are very much like those of our specimens of *L. rufoviride*. The ejaculatory vesicle is, perhaps, a little larger in *L. genypteri*, but the lining of the ejaculatory vesicle and the point of entry of the pars prostatica into this vesicle are very similar. In both cases the pars prostatica passes over the dorsal wall of the vesicle and enters antero-dorsally. As Jones (1943) shows the point of entry in *L. rufoviride* to be almost directly dorsal, it seems certain that this character varies to some extent, and is not reliable as a generic character.

With regard to *Magniscyphus*, the 'cup- or bowl-shaped' forebody is merely a variation of the ventro-cervical groove, which is common in many species of *Lecithochirium* (according to our definition). Indeed, a similar condition can be seen in fig. 38 of Looss (1908), in which he figures *L. musculus*. The occurrence of so-called prostatic cells around the hermaphroditic duct requires histochemical confirmation, as this may have been a case of the misinterpretation of the small gland-cells which commonly occur within the sinus-sac of hemiuroids. If these cells are prostatic, then it is more likely that they are associated with the distal extremity of the pars prostatica, which occasionally extends into the base of the sinus-sac. We do not consider that the presence of these cells is sufficient reason to substantiate the existence of *Magniscyphus* as a distinct genus from *Sterrhurus*, and hence *Lecithochirium*. In their useful work on *Lecithochirium*, Nasir & Diaz (1971), in addition to including *Sterrhurus*, *Separogermiductus* and *Magniscyphus* as synonyms of *Lecithochirium*, also considered *Synaptobothrium* and *Plerurus* likewise. We believe that Nasir & Diaz (1971) went too far with their synonymies, and that *Synaptobothrium* and *Plerurus* are valid genera.

BRACHYPHALLUS Odhner, 1905 [t(w,s)]

Body-surface plicated; plications may be crenulate. Presomatic pit present; circular or oval; deep; glandular. Seminal vesicle bipartite; anterior part small, posterior part large; thin-walled; occurring mostly in forebody. Pars prostatica tubular. Temporary sinus-organ may be seen. Vitellarium two lateral masses; entire, irregularly lobed or indistinctly three- and four-lobed. Parasitic in gut (stomach) of marine and migratory teleosts.

TYPE-SPECIES. *Brachyphallus crenatus* (Rudolphi, 1802) [by original designation].

COMMENT. The terminal genitalia were described in detail by Lander (1904) and Slusarski (1958), and we agree that a glandular ejaculatory (prostatic) vesicle is present.

CATARINATREMA Teixeira de Freitas & Santos, 1971

May bear papillae on ecsoma. Presomatic pit present. Muscular pad present anterior to oral sucker. Seminal vesicle bipartite; in forebody. Pars prostatica tubular. Vitellarium two masses of three and four short, digitiform lobes. Parasitic in stomach and intestine of marine teleosts.

TYPE-SPECIES. *Catarinatrema verrucosum* Teixeira de Freitas & Santos, 1971 [by original designation].

CYATHOLECITHOCHIRIUM Yamaguti, 1970

Body-surface smooth. Muscular 'shoulder-pads' present. Pre-oral accessory sucker absent. Seminal vesicle bipartite; anterior part with thick wall; in forebody. Pars prostatica may be partly within sinus-sac. Vitellarium seven digitiform lobes in two groups of three and four. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Cyatholecithochirium gymnothoracis* Yamaguti, 1970 [by original designation].

DISSOSACCUS Manter, 1947

Ecsoma well developed. Body-surface smooth. Seminal vesicle in two parts separated by narrow duct; one part normally mainly anterior and other mainly posterior to ventral sucker. Pars prostatica (?) tubular. Vitellarium two slightly indented masses. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Dissosaccus laevis* (Linton, 1898) [by original designation].

PLICATRIUM Manter & Pritchard, 1960

Papillae may occur on body-surface. Presomatic pit absent. Seminal vesicle bipartite; in forebody. Pars prostatica tubular. Large, eversible genital atrium present; wrinkled or convoluted when everted. Vitellarium seven digitiform lobes. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Plicatrium lycodontis* (Myers & Wolfgang, 1953) [by monotypy].

PROLECITHOCHIRIUM Yamaguti, 1970

Ecsoma reduced. Body-surface smooth. Presomatic pit absent. Seminal vesicle tubular; convoluted and widening posteriorly; in forebody. Pars prostatica tubular. Vitellarium two compact masses. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Prolecithochirium pterois* Yamaguti, 1970 [by original designation].

COMMENT. This genus has many of the characteristics of *Lecithochirium*; but apparently lacks lobation of the vitellarium.

PSEUDODINOSOMA Yamaguti, 1970

Ecsoma well developed. Body-surface with crenulate plications (? giving 'scaley' appearance). Presomatic pit absent. Seminal vesicle in two parts separated by narrow duct; one part (convoluted) anterior and other (claviform) posterior to ventral sucker. Pars prostatica tubular. Vitellarium two slightly indented masses. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Pseudodinosoma macrorchis* Yamaguti, 1970 [by original designation].

TRICOTYLEDONIA Fyfe, 1954 [n(w,s)]

Grassitrema Yeh, 1955

Body-surface smooth. Muscular 'shoulder-pads' present. Presomatic pit absent. Pre-oral accessory sucker present. Seminal vesicle bipartite; posterior part elongate; anterior to posterior margin of ventral sucker. Pars prostatica vesicular; partly enclosed by sinus-sac; leads into small, aglandular ejaculatory vesicle; connected to seminal vesicle by short, aglandular duct. Vitellarium seven digitiform lobes. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Tricotyledonia genypteri* Fyfe, 1954 [by original designation].

Subfamily **LETHADENINAE** Yamaguti, 1971

Ecsoma well developed. Body-surface smooth. Pre-somatic pit absent. Testes oblique. Seminal vesicle oval; thick-walled; in forebody. Pars prostatica vesicular; with muscular wall; external gland-cells absent or weakly developed; separated from seminal vesicle by aglandular duct and from sinus-sac by long ejaculatory duct. Sinus-sac small; not containing ejaculatory or prostatic vesicle. Sinus-organ (?) present (? temporary); small. Genital atrium short. Vitellarium two symmetrical, unlobed, oval masses. Excretory arms not united in forebody. Parasitic in stomach of marine teleosts.

LETHADENA Manter, 1947

Defined as subfamily.

TYPE-SPECIES. *Lethadena profunda* (Manter, 1934) [by original designation].

PLERURINAE subfam. nov.

Body small; spindle-shaped to cylindrical. Ecsoma reduced or well developed. Body-surface smooth, or occasionally with crenulate plications giving a scaley appearance. Presomatic pit absent, except in *Synaptobothrium*. Prepharynx absent. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present. Gut-caeca terminate blindly inside ecsoma. Testes pre-ovarian; symmetrical to tandem, usually oblique. Seminal vesicle elongate, saccular and constricted into two, three or four sections; thin-walled, although certain sections may have thicker walls; in forebody or partly in hindbody. Pars prostatica vesicular or tubular; may be partly enclosed by muscles of sinus-sac; commonly linked to seminal vesicle by aglandular duct. Sinus-sac apparently absent or poorly developed; when present usually of 'open'-type. Permanent sinus-organ absent. Ejaculatory (prostatic) vesicle absent. Hermaphroditic duct commonly vesicular proximally and tubular distally. Genital atrium usually deep, but may be shallow. Genital pore mid-ventral in forebody. Ovary entire or lobed. Laurer's canal absent. Canalicular and blind seminal receptacles absent. Juel's organ present. Uterine seminal receptacle present. Uterus convoluted; passing back from ovary into ecsoma and then forward into forebody. Vitellarium post-ovarian; composed of two, four- and three-lobed, masses; the lobes being small to digitiform. Excretory vesicle Y-shaped; arms united in forebody. Parasitic in stomach of marine teleosts.

COMMENT. It is important, in this group, to distinguish between a vesicular pars prostatica and an ejaculatory (prostatic) vesicle. An ejaculatory vesicle occurs in the Lecithochiriinae, lacks external prostatic cells, is normally entirely enclosed within a distinct sinus-sac, and is present together with a normal pars prostatica which occurs externally to, or occasionally partly within, the sinus-sac. The vesicular pars prostatica of the Plerurinae varies from being completely outside the sinus-sac, if it is present, to being only partly enclosed by the muscles of a weakly developed sinus-sac of the 'open'-type.

Key to Plerurinae

1.	A.	Seminal vesicle tripartite in forebody, anterior and middle sections with thick, muscular wall	***VOITREMA***
	B.	Seminal vesicle saccular to 4-lobed or tubular, thin-walled	2
2.	A.	Seminal vesicle in forebody	3
	B.	Seminal vesicle at least partly extended into hindbody	4
3.	A.	Presomatic pit absent; vitelline lobes digitiform	***PLERURUS***
	B.	Presomatic pit present; vitelline lobes short	***SYNAPTOBOTHRIUM***
4.	A.	Body-surface has 'scaley' appearance	***DINOSOMA***
	B.	Body-surface smooth	***ADINOSOMA***

PLERURUS Looss, 1907 [t(w,s)]

Paraplerurus Fischthal & Kuntz, 1963
Merlucciotrema Yamaguti, 1971

Ecsoma reduced or well developed. Body-surface smooth. Testes symmetrical to oblique. Seminal vesicle in forebody; elongate; saccular, two-, three- or four-lobed; often sigmoid; thin-walled. Pars prostatica vesicular; may be linked to seminal vesicle by short aglandular duct (some authors maintain that this is a tubular region of the pars prostatica). Sinus-sac apparently absent or poorly developed and of 'open'-type. Hermaphroditic duct tubular; deep; possibly eversible. Ovary oval to lobed. Vitelline lobes tubular to digitiform.

TYPE-SPECIES. *Plerurus digitatus* (Looss, 1899) [by original designation].

COMMENT. Yamaguti (1970) points out that Looss (1908) figures a large oval seminal receptacle in the type-species, and suggests that what Looss actually saw was a uterine seminal receptacle. We confirm that a uterine seminal receptacle does occur in this species. Juel's organ has been described in *P. longicaudatus* (Yamaguti, 1953) by Madhavi & Rao (1974) and we have observed it in the type-species.

Owing to its close phylogenetic relationship (see Fig. 9) with the Lecithochiriinae, we wondered whether the vesicular modification of the ejaculatory duct in this group might be a prostatic vesicle rather than a vesicular pars prostatica. Our observations of the type-species of this genus indicate that the structure present is a vesicular pars prostatica (see definition; p. 48). This is not really surprising, if our suggestions as to its possible function are correct, because in the absence of a sinus-sac, there is no functional requirement for a prostatic vesicle.

We have included *Merlucciotrema*, which Yamaguti (1971) based upon Manter's specimen of *Sterrhurus praeclarus* Manter, 1934, as a synonym of *Plerurus*, because it appears to differ only in the reduced nature of the ecsoma and in that the vitelline lobes appear to be separated by narrow vitelline ducts. The size of the ecsoma is a variable feature in many hemiurid genera, even when contraction is taken into account, and Manter's original illustration suggests some evidence that the ecsoma of this species might be invaginated further than he indicates.

ADINOSOMA Manter, 1947

Body-surface smooth. Testes oblique. Seminal vesicle large, saccular, bipartite; postero-dorsal to ventral sucker. Pars prostatica vesicular, but elongate; connected to seminal vesicle by long, aglandular duct. Sinus-sac apparently absent. Hermaphroditic duct long, with poorly developed hermaphroditic vesicle proximally. Ovary unlobed. Vitellarium two indented or lobed masses.

TYPE-SPECIES. *Adinosoma robustum* (Manter, 1934) [by original designation].

COMMENT. This genus includes *A. hawaiiense* (Yamaguti, 1970) n. comb., a species which was originally placed in the genus *Dinosoma*.

DINOSOMA Manter, 1934 [T(w,s); n(w,s)]

Body-surface with crenulate plications, giving 'scaley' appearance. Testes symmetrical to tandem. Seminal vesicle postero-dorsal to ventral sucker; saccular, bipartite or wide; sinuous. Pars prostatica vesicular; may be connected to seminal vesicle by long, aglandular duct. Sinus-sac apparently absent. Hermaphroditic duct long, narrow; with small vesicle proximally. Ovary oval. Vitellarium two indented or lobed masses.

TYPE-SPECIES *Dinosoma rubrum* Manter, 1934 [by original designation].

SYNAPTOBOTHRIUM von Linstow, 1904 [t(w,s)]

Body-surface smooth. Presomatic pit present; circular or oval; deep; glandular. Testes oblique. Seminal vesicle bipartite (? or tripartite); anterior part small, posterior part long; thin-walled; occurring mostly in forebody, but may extend dorsal to ventral sucker. Pars prostatica tubular with wide lumen; may extend into base of sinus-sac. Sinus-sac weakly developed; of 'open'-type. Ovary oval. Vitellarium two lateral masses with three and four short lobes. Eggs may be reniform.

TYPE-SPECIES. *Synaptobothrium caudiporum* (Rudolphi, 1819) [syn. *S. copulans* von Linstow, 1904 – type by monotypy].

COMMENT. The sinus-sac in this genus is weakly developed and of the 'open'-type, and an ejaculatory (prostatic) vesicle is absent. We have, therefore, included it in the Plerurinae. The wide pars prostatica may extend into the base of the 'open' sinus-sac. *Lecithochirium apharei* Yamaguti, 1970, probably belongs to this genus.

(?) *VOITREMA* Yamaguti, 1971

[Inadequately known.] Body-surface (?). Testes oblique. Seminal vesicle tripartite; in forebody; anterior and middle sections with thick, muscular wall. Pars prostatica vesicular; may be partly enclosed by muscles of (?) sinus-sac; attached to seminal vesicle by short (?) aglandular duct. Sinus-sac (?) weakly developed; with diffuse musculature; of 'open'-type. Genital atrium sac-like. Ovary elongate oval. Vitelline lobes digitiform.

TYPE-SPECIES. *Voitrema amplum* (Manter, 1961) [by original designation].

COMMENT. This is a questionable genus based upon one inadequately described specimen.

Subfamily **PULMOVERMINAE** Sandars, 1961

Ecsoma reduced. Body-surface smooth (? spines reported within suckers). Presomatic pit absent. Testes tandem to oblique. Seminal vesicle tubular; long; thick-walled; reaches to or almost to level of testes. Pars prostatica short; vesicular; partly enclosed by sinus-sac. Sinus-sac present; not enclosing ejaculatory or prostatic vesicle. Sinus-organ variable in length, (? temporary). Genital atrium small. Ovary occasionally divided into dorsal and ventral lobes. Vitellarium two lateral, closely aligned masses; normally with three and four lobes. Excretory arms united in forebody. Parasitic in lung of sea-snakes.

PULMOVERMIS Coil & Kuntz, 1960

Hydrophitrema Sandars, 1960
Laticaudatrema Telford, 1967

Defined as subfamily.

TYPE-SPECIES. *Pulmovermis cyanovitellosus* Coil & Kuntz, 1960 [by original designation].

Family **HIRUDINELLIDAE** Dollfus, 1932

Botulidae Guiart, 1938
Lampritrematidae Yamaguti, 1940
Mediolecithidae Oshmarin, 1968
[Includes: Profundiellinae Skrjabin, 1958]

Body large; stout or elongate; contractile. Ecsoma absent. Body-surface smooth; may be papillate in forebody or wrinkled. Oral and ventral suckers well developed; latter in anterior half of body. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' present. Gut-caeca terminate blindly or form uroproct; sometimes fuse subterminally forming cyclocoel; usually diverticulate. Testes two; in tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular; normally thin-walled, occasionally partly thick-walled; convoluted in forebody. Pars prostatica well developed; tubular; usually long. Ejaculatory duct long; muscular; surrounded by muscular 'cirrus-sac'; opens into genital atrium through well-developed conical to cylindrical 'cirrus'. Hermaphroditic duct, sinus-sac and sinus-organ absent. Genital atrium large; usually capable of being everted. Genital pore mid-ventral in forebody. Ovary oval; post-testicular; in middle or anterior half of hindbody. Laurer's canal and uterine seminal receptacle normally present. Juel's organ and blind or canalicular seminal receptacle absent. Uterus descending ventrally and ascending more dorsally; coiled mainly at level of vitellarium, but often extending more anteriorly into pre-ovarian region; mainly inter-caecal, occasionally reaching extra-caecally; metraterm opens into genital atrium directly or through a papilla-like organ situated immediately posterior to 'cirrus'. Eggs numerous; small; without filaments. Vitellarium composed of from two to numerous long, straight or convoluted, branched tubules; mainly post-ovarian; inter- or extra-caecal. Excretory vesicle Y-shaped; arms initially dorso-ventrally oriented, convoluted, united in forebody. Parasitic in stomach (occasionally on gills) of large, carnivorous, marine teleosts.

COMMENT. In our opinion this family contains three monotypic genera which cannot be distinguished at the subfamily level. It is possible that *Distoma gigas* Nardo, 1827, from the stomach of *Luvarus imperialis* is a fourth genus; but, as suggested by Gibson & Bray (1977), there is some evidence that this species may be a sclerodistomid (see p. 113).

Key to Hirudinellidae

1. A. Body stout, elongate or keyhole-shaped; uroproct present; 'cirrus-sac' small, globular; seminal vesicle entirely thin-walled 2
   B. Body slender, elongate; uroproct absent; 'cirrus-sac' large, elongate; distal part of seminal vesicle with muscular wall . . . . *LAMPRITREMA*

2. A. Vitellarium in two lateral fields between levels of testes and mid-hindbody; uterus mainly inter-caecal, post-ovarian, at level of vitellarium . . . . . . *HIRUDINELLA*
   B. Vitellarium massed close to ventral surface, inter-caecal between ovary and posterior extremity; uterus reaching extra-caecally, mainly in anterior hindbody . . *BOTULUS*

HIRUDINELLA de Blainville, 1828 [t(w,s)]

Hirudinella Garcin, 1730 [Pre-Linnaean; see Gibson, 1976]
Uroproctinella Skrjabin & Guschanskaja, 1957

Body stout, elongate or keyhole-shaped. Body-surface often transversely wrinkled. Uroproct present; gut-caeca may fuse sub-terminally in older specimens forming cyclocoel. Testes symmetrical to oblique; in anterior hindbody. Seminal vesicle thin-walled throughout its length. 'Cirrus-sac' relatively small; globular. 'Cirrus' cone-shaped to digitiform. Genital atrium capable of being everted through genital pore. Ovary in anterior hindbody. Uterus mainly inter-caecal; coils extending posteriorly from ovary to near posterior limit of vitellarium. Vitellarium in two lateral fields between testes and middle of hindbody. Parasitic in stomach of large carnivorous, marine teleosts (usually scombroids).

TYPE-SPECIES. *Hirudinella ventricosa* (Pallas, 1774) [syn. *H. clavata* (Menzies, 1791) – type by monotypy].

COMMENT. As discussed by Gibson (1976), it is likely that this genus is monotypic.

BOTULUS Guiart, 1938 [T(w,s); t(w,s)]

Profundiella A. S. Skrjabin, 1958
Mediolecithus Oshmarin, 1968

Body normally stout. Uroproct present. Testes symmetrical to oblique; in anterior hindbody; large. Seminal vesicle thin-walled throughout its length; tubular and convoluted [or (?) globular (in *Profundiella skrjabini* A. S. Skrjabin, 1958)]. 'Cirrus-sac' small; globular. 'Cirrus' cone-shaped to digitiform. Genital atrium often everted through genital pore. Ovary in anterior hindbody. Uterus reaching extra-caecally in anterior hindbody. Vitellarium a densely tangled mass of tubeles in one ventral, inter-caecal field between ovary and posterior extremity. Parasitic in stomach of large, carnivorous, marine teleosts (*Alepisaurus*) and (?) accidentally in piscivorous sharks.

TYPE-SPECIES. *Botulus microporus* (Monticelli, 1889) [syn. *B. alepidosauri* Guiart, 1938 – type by monotypy].

COMMENT. The two specimens of *Botulus alepidosauri* originally described by Guiart (1938), according to his manuscript, were in poor condition (they were dried out) which accounts for the inadequate description. We have been able to examine specimens of *Botulus* from the type-host, *Alepisaurus ferox*, and to refine the concept of this genus (see Gibson & Bray, 1977). We have also examined the type-specimens of *Distomum microporum* Monticelli, 1889, present in the collections of the British Museum (Natural History). These specimens were recovered from the type-host (*A. ferox*) and type-locality (off Madeira) of *B. alepidosauri*. Although *D. microporum* has been listed as a species of *Hemiurus* by some authors (Looss, 1899; Yamaguti, 1971), our examination has convinced us that it is a senior synonym of *B. alepidosauri*. The morphology of *Botulus microporus* is described in detail elsewhere (Gibson & Bray, 1977).

Profundiella was originally erected for a new species, *P. skrjabini*, from *Alepisaurus aesculapius* (which may be synonymous with *A. ferox*), in the Pacific Ocean by A. S. Skrjabin (1958). There appears to be no significant difference between this genus and *Botulus*, except for the reported presence of a globular seminal vesicle in the former. A second species, *P. alepisauri*, was described by Parukhin & Nikolaeva (1967) from *Alepisaurus* sp. in the Gulf of Mexico (*A. ferox* appears to be the only species of *Alepisaurus* recorded in this region); but this species possesses a seminal vesicle which is tubular and coiled. Examination of specimens of *Botulus* from *Alepisaurus ferox* from off Miami Beach, Florida, show that they appear to be indistinguishable from *B. microporus*. It seems probable that the apparent globular seminal vesicle of *P. skrjabini* may in fact be a tightly coiled, tubular form, as a tubular seminal vesicle is the normal condition in primitive hemiuroids. Stunkard (1965) also considered *Profundiella* as a synonym of *Botulus*, but it was listed separately by Yamaguti (1971).

In agreement with Parukhin & Nikolaeva (1974), we are of the opinion that *Mediolecithus pacificus* Oshmarin, 1968, belongs to *Botulus*. One specimen was described by Oshmarin from *Lamna cornubica*, a piscivorous shark. It is likely that this was an accidental infestation, as *Alepisaurus* is the normal host of *Botulus*.

LAMPRITREMA Yamaguti, 1940 [T(s)]

Hirudinelloides Gaevskaja & Kovaleva, 1977

Body elongate; slender. Papillae present on forebody. Uroproct absent. Testes in tandem; near middle of hindbody. Most of seminal vesicle thin-walled, but distal portion forms thick-walled, muscular 'pars musculosa'. Thick-walled pars prostatica lies ventral to posterior portion of 'cirrus-sac'. Male duct leads into 'cirrus-sac' some distance from its posterior extremity. 'Cirrus-sac' large; elongate; club-shaped. 'Cirrus' long or short; capable of being extruded some distance through genital pore. Genital atrium deep. Ovary near middle of hindbody. Laurer's canal (?) absent. Seminal receptacle (?) small; enclosed in Mehlis' gland [see below]. Uterus extends back to near posterior limit of vitellarium; mainly coiled inter-caecally in post- and pre-ovarian regions of hindbody. Vitellarium a pair of lateral tubules with short dorsal branches; mainly extra-caecal; passing posteriorly from ovary to about half-way to posterior extremity. Excretory arms appear to unite in forebody (cf. Yamaguti, 1940). Parasitic in stomach (? occasionally on gills) of marine teleosts (*Lampris*, *Brama* and *Thyrsites*). Immature forms recorded from salmonids (stomach, oesophagus or gills).

TYPE-SPECIES. *Lampritrema miescheri* (Zschokke, 1890) [syn. *L. nipponicum* Yamaguti, 1940 – type by original designation].

COMMENT. We considered separating *Lampritrema* from *Hirudinella* and *Botulus* at the subfamily level, but there are no morphological differences which one could definitely consider to be important at the subfamily level.

Notwithstanding the descriptions of *Lampritrema atlanticum* Delyamure & Serdyukov, 1970, *L. hawaiiense* Yamaguti, 1970, and *Hirudinelloides elongatus* Gaevskaja & Kovaleva, 1977, we consider this genus to be monotypic (see Gibson & Bray, 1977). *L. savalai* Zaidi & Khan, 1977, is clearly a hemiurid.

Yamaguti (1940) stated that Laurer's canal was absent in *Lampritrema nipponicum* and that a small seminal receptacle was present inside Mehlis' gland. We question the absence of Laurer's canal in this species, as it is present in all other primitive hemiuroids, and the small size (up to 105 µm) and location of the seminal receptacle suggests that its presence and nature is questionable: we would expect a uterine seminal receptacle to be present. Neither of these features were commented upon by Margolis (1962) in his redescription of this species.

Family **ISOPARORCHIIDAE** Travassos, 1922

Body large; stout; dorso-ventrally flattened. Ecsoma absent. Body-surface smooth. Oral and ventral suckers small. Pharynx well developed. Oesophagus short. 'Drüsenmagen' absent. Gut-caeca sinuous; terminate blindly near posterior extremity. Testes two; symmetrical; pre-ovarian; in anterior hindbody. Seminal vesicle small; thin-walled; tubular; winding in forebody. Pars prostatica tubular. Ejaculatory duct within sinus-sac. Sinus-sac weakly developed; composed of diffuse musculature. Hermaphroditic duct short; opens into genital atrium through stout sinus-organ. Genital atrium with pair of concentric folds in its wall; capable of being extruded through genital pore [see Fig. 2]. Genital pore mid-ventral in forebody. Ovary tubular; well posterior to testes. Laurer's canal present; may be slightly dilated proximally forming small rudimentary seminal receptacle. Uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus pre-ovarian; mainly coiled in hindbody. Eggs numerous; small; non-filamented. Vitellarium tubular; with dendritic branches arising from about six collecting ducts; post-ovarian. Excretory vesicle Y-shaped; arms come close together dorsal to pharynx, but do not unite. Parasitic in swim-bladder of physostomatous teleosts in freshwater (Asia and Australasia).

ISOPARORCHIS Southwell, 1913 [t(w,s)]

Leptolecithum Kobayashi, 1915

Defined as family.

TYPE-SPECIES. *Isoparorchis hypselobagri* (Billet, 1898) [syn. *I. trisimilitubis* Southwell, 1913 – type by original designation].

Family **LECITHASTERIDAE** Odhner, 1905

Lobatovitelliovariidae Yamaguti, 1965

Body usually small; normally spindle-shaped, occasionally elongate. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed; ventral sucker normally in anterior half of body. Muscular flange or flanges may be present immediately posterior to ventral sucker. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' normally present. Gut-caeca usually terminate blindly, but occasionally unite forming cyclocoel. Presomatic pit and ventro-cervical groove absent. Testes two, occasionally one; in tandem; oblique or symmetrical; usually, but not always, pre-ovarian; in hindbody. Seminal vesicle generally thin-walled, occasionally muscular; oval, tubular or constricted into portions; in fore- or hindbody. Pars prostatica usually tubular, occasionally vesicular; may be linked to seminal vesicle by aglandular tube. Ejaculatory duct long, short or absent. Hermaphroditic duct present. Ejaculatory (prostatic) vesicle absent. Sinus-sac usually present; well or poorly developed; occasionally absent. Permanent sinus-organ normally absent, but hermaphroditic duct is often protruded to form temporary sinus-organ. Genital atrium large, small or absent. Ovary usually post-testicular; oval or four- (occasionally three-) lobed. Usually only blind seminal receptacle present (normally large, thick-walled and situated dorsal or antero-dorsal to ovary) and Laurer's canal, Juel's organ and both uterine or canalicular seminal receptacles absent; occasionally only Juel's organ and uterine seminal receptacle present; rarely only Laurer's canal and canalicular seminal receptacle present. Uterus mainly post- to entirely pre-ovarian; main bulk rarely extends into forebody. Eggs numerous; small; rarely filamented. Vitellarium commonly seven-lobed; occasionally six, eight or double these numbers (sometimes branched) lobes often in rosette arrangement; usually immediately post-ovarian, occasionally pre-ovarian or at level of ovary. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic in gut, especially intestine, of marine teleosts.

Key to Lecithasteridae

1. A. Uterine seminal receptacle present . . . . . . **HYSTEROLECITHINAE** (p. 104)
B. Uterine seminal receptacle absent 2
2. A. Uterus entirely or almost entirely pre-ovarian; hermaphroditic duct appears to be continuation of uterus; Laurer's canal may be present . **TRIFOLIOVARIINAE** (p. 109)
B. Uterus partly post-ovarian; hermaphroditic duct normal 3
3. A. Muscular ventro-lateral flange or flanges present immediately posterior to ventral sucker **QUADRIFOLIOVARIINAE** (p. 108)
B. Muscular ventro-lateral flange or flanges absent immediately posterior to ventral sucker . 4
4. A. Seminal vesicle in forebody or dorso-lateral to ventral sucker (in one or two species of *Lecithaster* it may extend into the anterior hindbody, but these can be distinguished from the macradeninines by the well-developed nature of the sinus-sac) . . . 5

B. Seminal vesicle entirely in hindbody; pars prostatica and/or ejaculatory duct long; sinus-sac small or poorly developed; usually parasitic in *Acanthurus* spp.
MACRADENININAE (p. 105)
5. A. Sinus-sac relatively well developed; vitellarium post-ovarian . **LECITHASTERINAE** (p. 102)
B. Sinus-sac apparently absent; genital atrium sucker-like; vitellarium pre-ovarian
PROLECITHINAE (p. 107)

Subfamily LECITHASTERINAE Odhner, 1905

Lecithophyllinae Skrjabin & Guschanskaja, 1954

Caeca terminate blindly. Testes two, occasionally one; pre-ovarian. Seminal vesicle in forebody, dorsal to ventral sucker or, occasionally, in anterior hindbody. Pars prostatica short to medium in length. Ejaculatory duct absent or short. Sinus-sac well developed. Permanent sinus-organ absent. Ovary entire or four-lobed. Blind seminal receptacle normally large; usually dorsal to ovary. Uterus reaches to post-ovarian region. Vitellarium seven (rarely six or eight) oval to digitiform lobes in rosette or two linked groups of three and four; immediately post-ovarian; occasionally antero-posteriorly oriented. Excretory arms united in forebody or not. Normally parasitic in intestine or stomach of marine teleosts.

Key to Lecithasterinae

1. A. Testis single . . . . *MONORCHIAPONURUS*
B. Testes two 2
2. A. Vitelline lobes tubular . . . . *QADRIANA* (inadequately described)
B. Vitelline lobes tear-shaped to globular 3
3. A. Ovary lobed, usually with four lobes; vitelline lobes tear-shaped . . . . *LECITHASTER*
B. Ovary oval to globular; vitelline lobes globular 4
4. A. Genital atrium present . . . . *LECITHOPHYLLUM*
B. Genital atrium small or absent . . . . *APONURUS*

LECITHASTER Lühe, 1901 [n(w,s)]

Testes two; obliquely symmetrical; usually oval, but occasionally lobed. Seminal vesicle saccular to elongate and sinuous; in forebody, dorsal to ventral sucker or, occasionally, in anterior hindbody. Sinus-sac oval. Genital atrium short. Ovary normally four-lobed. Seminal receptacle large, globular; dorsal to ovary. Vitellarium a radiating mass of seven tear-shaped lobes. Excretory arms apparently not united in forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Lecithaster confusus* Odhner, 1905 [by subsequent designation – Odhner, 1905].

COMMENT. Dawes (1947) lists *Leptosoma* Stafford, 1904 [*nec* Desmarest, 1825; *nec* Travassos, 1920; etc.; etc.] as a synonym of *Lecithaster*; but Stafford's description of *Leptosoma obscurum* is not adequate for a determination, even at the family-level. For this reason, therefore, and because: (1) *Leptosoma* was not mentioned by Miller (1941), who studied Stafford's material; (2) there are no specimens amongst Stafford's material in the National Museums of Canada, Ottawa; and (3) lecithasterids do not appear to be normal parasites of *Lophius*, from which *Leptosoma* was recorded; we consider that this genus is unrecognizable.

APONURUS Looss, 1907

Brachadena Linton, 1910
(?) *Mordvilkoviaster* Pigulewsky, 1938

Testes two; tandem to oblique. Seminal vesicle saccular; in forebody or occasionally dorsal to ventral sucker. Hermaphroditic duct usually tubular, occasionally bipartite. Sinus-sac oval to elongate-oval. Genital atrium absent, or occasionally small. Ovary oval or globular. Seminal receptacle small to large; (?) ventral or dorsal to anterior region of ovary. Vitellarium usually seven globular to slightly elongate lobes; in lateral, occasionally antero-posteriorly oriented, groups of three and four. Excretory arms united in forebody. Parasitic in stomach (occasionally intestine) of marine teleosts.

Type-species. *Aponurus laguncula* Looss, 1907 [by monotypy].

Comment. The validity of *Aponurus* as a distinct genus from *Lecithophyllum* has been a matter of some discussion (see Margolis, 1958). The two genera differ in the presence and absence of a distinct genital atrium. As this is a contractile organ, its use as an important taxonomic criterion should be treated with caution. In this case the character does appear to be of value, as it is a deep and apparently consistent feature in species of *Lecithophyllum*. It would not be surprising, however, if future workers discovered that, with regard to this feature, the two genera tend to grade into one another: indeed, *Lecithophyllum hawaiiense* Yamaguti, 1970, may be such a case in point. Yamaguti (1953) used the nature of the hermaphroditic duct to distinguish these two genera: species of *Lecithophyllum* normally possess an hermaphroditic duct which is bipartite, whereas in *Aponurus* it is supposed to be uniform throughout its length. Yamaguti's (1970) figure of *Aponurus acanthuri* Manter & Pritchard, 1960, which he placed in *Lecithophyllum* despite the extremely small size of the genital atrium, and Overstreet's (1973) figure of *A. pyriformis* (Linton, 1910) indicate that these species have bipartite hermaphroditic ducts.

With regard to the status of *Brachadena* Linton, 1910, Yamaguti (1953, 1958, 1971) considered this genus a synonym of *Lecithophyllum*, whereas Margolis (1958) believed it to be distinct on the basis of a central union of the vitelline lobes. Contrary to the work of Fischthal & Kuntz (1964c), which showed that a small genital atrium is present in the type-species, *B. pyriformis* Linton, 1910, Overstreet (1973) demonstrated that there is no distinct genital atrium present: Yamaguti's (1971) figure of the paratype also indicated that there is no genital atrium present. Overstreet's work showed that the type-species has an antero-posteriorly oriented vitellarium, the three- and four-lobed groups of which being united by a short duct. In view of the questionable validity of *Aponurus* itself, we feel that any variations in the nature and orientation of the vitellarium and in the hermaphroditic duct of *Brachadena pyriformis*, as compared with other species of *Aponurus*, should be regarded as being of only specific value.

Aponurus priacanthi Yamaguti, 1970, does not appear to be a lecithasterine. A uterine seminal receptacle and possibly a Juel's organ are shown in Yamaguti's figure of this species.

We have tentatively included *Mordvilkoviaster* Pigulewsky, 1938, as a synonym of *Aponurus*, as both Looss (1908) and Pogoreltseva (1952) have described *Lecithaster galeatus* Looss, 1907, the type-species, as having a round ovary. Skrjabin & Guschanskaja (1954) and Yamaguti (1971) consider *Mordvilkoviaster* to be a synonym of *Dichadena* Linton, 1910; but we believe that the sinus-sac is too well developed, the seminal vesicle too anterior and the pars prostatica too short for it to be considered a macradeninine.

LECITHOPHYLLUM Odhner, 1905 [t(w,s)]

Testes two; obliquely tandem to symmetrical. Seminal vesicle saccular; in forebody or dorsal to ventral sucker. Hermaphroditic duct apparently bipartite. Sinus-sac elongate. Genital atrium present; generally deep. Ovary oval or globular. Seminal receptacle large; dorsal to ovary. Vitellarium seven globular lobes, in lateral groups of three and four. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

Type-species. *Lecithophyllum botryophoron* (Olsson, 1868) [by original designation].

Comment. Brinkmann (1977), in his detailed redescription of the type-species, described and figured a sinus-organ. As with other species in this family, this structure is temporary: it is not present in our material of this species (fixed in glacial acetic acid). A temporary sinus-organ, however, can be extruded in artificially relaxed, slowly fixed or frozen material.

(?) *MONORCHIAPONURUS* Fischthal & Nasir, 1974

Testis single. Seminal vesicle saccular; in forebody. Sinus-sac elongate. Hermaphroditic duct tubular. Genital atrium absent. Ovary oval. Seminal receptacle pre-ovarian; postero-dextral to testis. Vitellarium seven globular lobes. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Monorchiaponurus hemirhamphi* Fischthal & Nasir, 1974 [by original designation].

COMMENT. This genus is known from only one specimen. As the absence of one testis is not a rare feature amongst bi-testicular digeneans, it is possible that this specimen is merely an abnormal example of *Aponurus*. More specimens, as in the case of *Monorchimacradena* Nahhas & Cable, 1964, are required before this genus can be fully accepted. In listing this genus independently of *Aponurus*, we are assuming that the seminal receptacle, which is rather far anterior for a lecithasterid, has not been confused with the second testis.

(?) *QADRIANA* Bilqees, 1971

[Inadequately described.] Testes two; tandem; postero-lateral to ventral sucker. Seminal vesicle saccular; in forebody. Ovary oval. 'Seminal receptacle not obvious.' Vitellarium 'composed of several tubes'. Uterus extra-caecal in hindbody. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Qadriana fusiformis* Bilqees, 1971 [by monotypy].

Subfamily **HYSTEROLECITHINAE** Yamaguti, 1958

Body small; elongate to spindle-shaped. Ventral sucker in middle or anterior half of body. Gut-caeca end blindly near posterior extremity. Testes two; oval; symmetrical to obliquely tandem; pre-ovarian; in anterior half of hindbody. Seminal vesicle usually tubular, occasionally elongate saccular; in forebody. Pars prostatica usually tubular, occasionally vesicular; short. Sinus-sac present; often weakly developed; occasionally of open-type. Permanent sinus-organ absent; temporary sinus-organ may form. Hermaphroditic duct present within sinus-sac. Genital atrium small or absent. Ovary oval; in anterior or posterior half of hindbody. Laurer's canal and blind or canalicular seminal receptacle absent. Juel's organ and uterine seminal receptacle present [see below]. Uterus almost entirely in hindbody; mainly pre- to mainly post-ovarian. Eggs with or without filaments. Vitellarium seven (occasionally eight) oval to digitiform lobes; post-ovarian. Excretory arms united in forebody or not. Parasitic mainly in intestine or stomach of marine teleosts (usually perciform genera, especially acanthurids and pomacentrids).

COMMENT. There appears to have been some confusion between the genera of this subfamily and certain other lecithasterid genera. We have, therefore, taken our definitions only from species in which the presence of a uterine seminal receptacle or the absence of a blind or canalicular seminal receptacle has been indicated. Although Juel's organ has not been reported previously in this group, we found it to be well developed in a paratype specimen of *Hysterolecitha elongata* Manter, 1931, from the H. W. Manter Collection, which Dr M. H. Pritchard kindly allowed us to section. Yamaguti (1934) in his description of *Hysterolecithoides epinepheli* referred to a large seminal receptacle in addition to a uterine seminal receptacle, and in his (1942) description of *Hysterolecitha nahaensis* he referred to a small seminal receptacle in addition to a uterine seminal receptacle. Unless a similar variation to that present in the Derogeninae occurs in this subfamily, it is probable that the organ described by Yamaguti as a seminal receptacle is Juel's organ.

Key to Hysterolecithinae

1.	A.	Eggs filamented	*THULINIA*
	B.	Eggs without filaments	2
2.	A.	Excretory arms united in forebody; uterus mainly pre-ovarian . .	*HYSTEROLECITHA*
	B.	Excretory arms not united in forebody; uterus mainly post-ovarian	*HYSTEROLECITHOIDES*

COMMENT. In order to identify a genus from this subfamily, it is essential that eggs are teased from the body and that the anterior regions of the excretory system are examined. The latter normally necessitates sectioning. It is clear, in species where the excretory system has not been fully described, that there has been some confusion between *Hysterolecitha* and *Hysterolecithoides*. For example, although the excretory system was not fully described, Yamaguti (1971) placed *Hysterolecithoides pseudorosea* Bravo-Hollis, 1956, in the genus *Hysterolecitha*, despite the position of the ovary and the distribution of the uterus which suggested that Bravo-Hollis (1956) was correct.

HYSTEROLECITHA Linton, 1910 [n(w,s)]

Ventral sucker usually in anterior half of body; occasionally near middle. Seminal vesicle normally tubular; occasionally elongate saccular. Pars prostatica tubular; occasionally vesicular. Sinus-sac present; often weakly developed; may be of 'open'-type. Ovary normally in posterior half of hindbody; normally separated from testes by loops of uterus. Uterus usually mainly pre-ovarian; (?) occasionally mainly post-ovarian. Eggs without filaments. Excretory arms united in forebody.

TYPE-SPECIES. *Hysterolecitha rosea* Linton, 1910 [by original designation].

HYSTEROLECITHOIDES Yamaguti, 1934

Ventral sucker in middle of body. Seminal vesicle tubular. Pars prostatica tubular or vesicular. Sinus-sac oval. Ovary close to testes. Uterus mainly post-ovarian. Eggs without filaments. Excretory arms not united in forebody.

TYPE-SPECIES. *Hysterolecithoides epinepheli* Yamaguti, 1934 [by original designation].

THULINIA gen. nov.

Body elongate. Ventral sucker in anterior half of body. Gut-caeca end blindly near posterior extremity. Testes two; oval; obliquely tandem; separated from ventral sucker and ovary by loops of uterus. Seminal vesicle tubular; in forebody; may reach dorsally to ventral sucker. Pars prostatica tubular; short. Sinus-sac present; well developed. Permanent sinus-organ absent; temporary sinus-organ may form. Hermaphroditic duct present within sinus-sac. Genital atrium small. Genital pore mid-ventral near middle of forebody. Ovary oval; in posterior half of hindbody. Laurer's canal presumed absent. Canalicular or blind seminal receptacle absent. Juel's organ and uterine seminal receptacle presumed present. Uterus almost entirely in hindbody; coiled in pre- and post-ovarian fields. Eggs filamented (one filament at each end). Vitellarium seven (or eight) digitiform lobes; post-ovarian. Excretory vesicle Y-shaped; excretory arms united in forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Thulinia tinkeri* (Manter & Pritchard, 1960) n. comb.

COMMENT. We have erected this genus because of the presence of filaments on the eggs, a feature which we believe to be a good generic criterion. It is named after Mr Jan Thulin, University of Gothenburg, who has helped us with several aspects of our work.

Subfamily **MACRADENININAE** Skrjabin & Guschanskaja, 1954

Gut-caeca usually end blindly, but cyclocoel sometimes present. Testes two, occasionally one; oval; usually pre-ovarian, but may be at level of ovary or post-ovarian. Seminal vesicle in hindbody; saccular, tri-partite or tubular. Pars prostatica tubular; long. Ejaculatory duct usually long, but may be short or absent. Sinus-sac present; small; may be poorly developed. Permanent sinus-organ absent. Ovary four-lobed or oval. Blind seminal receptacle present. Uterus reaches to post-ovarian region. Vitellarium immediately anterior, at level of or immediately posterior to ovary; variable, commonly six- to eight-lobed, but may be seven branched lobes, or twelve or fourteen lobes, and group of lobes may be antero-posteriorly oriented. Excretory arms united in forebody or not. Parasitic in intestine or stomach of marine teleosts (normally *Acanthurus* spp.).

Key to Macradenininae

1. A. Vitellarium consisting of 6 to 8 (usually 7) tear-shaped or slightly branched lobes; seminal vesicle saccular (? or tubular) 2
B. Vitellarium consisting of 12 or more lobes (occasionally 7 basic lobes divided into about 40 secondary lobes) which may be tubular or globular; seminal vesicle tubular or tri-partite 5
2. A. Ovary 4-lobed . . . . *PSEUDODICHADENA*
B. Ovary unlobed 3
3. A. Testis single . . . . *MONORCHIMACRADENA*
B. Testes 2. 4
4. A. Testes at level of ovary; vitellarium antero-lateral to ovary; seminal vesicle (?) saccular or (?) tubular . . . . *DICHADENA*
B. Testes pre-ovarian; vitellarium post-ovarian; seminal vesicle saccular (? with constriction) *NEODICHADENA*
5. A. Seminal vesicle tubular; vitelline lobes elongate, in single group 6
B. Seminal vesicle tri-partite; vitelline lobes globular, in 2 groups, 7 anterior and 7 posterior to ovary . . . . *ACANTHURITREMA*
6. A. Testes post-ovarian; vitellarium 12 claviform lobes, ventral to ovary . *MACRADENINA*
B. Testes pre-ovarian; vitellarium essentially 7 lobes, but divided into about 40 secondary lobes, between ovary and seminal vesicle . . . . . . *MACRADENA*

COMMENT. We have retained all of the genera in this subfamily because of conflicting accounts of their morphology and in view of Yamaguti's (1971) examination of many of the holotypes; but it is likely that some of these forms will prove to be synonymous. Several of the genera require the study of fresh material before their validity can be confirmed, and a redescription of *Dichadena acuta* Linton, 1910, especially is needed. This subfamily appears to be almost entirely restricted to fishes of the genus *Acanthurus* from the central American region and Hawaii.

MACRADENINA Manter, 1947

Cyclocoel not reported. Testes tandem; post-ovarian. Seminal vesicle tubular; loosely coiled at level of ovary. Pars prostatica long. Ejaculatory duct (?) absent. Sinus-sac sub-cylindrical; may be incomplete posteriorly; appears to be protrusible. Ovary four-lobed; well forward in hindbody. Seminal receptacle globular; large; post-ovarian. Vitellarium twelve claviform, unbranched tubules; ventral to ovary. Excretory arms (?).

TYPE-SPECIES. *Macradenina acanthuri* Manter, 1947 [by original designation].

ACANTHURITREMA Yamaguti, 1970

Cyclocoel not reported. Testes tandem to oblique; pre-ovarian. Seminal vesicle tri-partite; posterior part large and spherical, middle part elongate elliptical, anterior part pyriform; connected to pars prostatica by aglandular duct; in anterior hindbody. Pars prostatica short. Ejaculatory duct absent. Sinus-sac thin, membranous; indistinct. Ovary four-lobed. Seminal receptacle large; antero-dorsal to ovary. Vitellarium fourteen globular lobes; seven anterior and seven posterior to ovary. Excretory arms not united in forebody.

TYPE-SPECIES. *Acanthuritrema multivitellosum* Yamaguti, 1970 [by original designation].

DICHADENA Linton, 1910

Cyclocoel (?) not reported (except in key by Yamaguti, 1971). Testes tandem; dorsal to ovary. Seminal vesicle sac-like (tubular according to Yamaguti, 1971); immediately pre-testicular. Pars prostatica long; dilate posteriorly. Ejaculatory duct similar in length to pars prostatica. Sinus-sac oval. Ovary oval [four-lobed according to Manter, 1947: specimens with four-lobed ovary described by Siddiqi & Cable, 1960, as *D. acuta*, now placed in *Pseudodichadena*]. Seminal receptacle between posterior margin of ovary and posterior testis. Vitellarium six or seven rounded to tear-shaped lobes; antero-lateral to ovary. Excretory arms (?).

TYPE-SPECIES. *Dichadena acuta* Linton, 1910 [by original designation].

MACRADENA Linton, 1910

Cyclocoel not reported. Testes tandem; pre-ovarian. Seminal vesicle tubular; coiled in anterior hindbody. Pars prostatica long. Ejaculatory duct about one quarter length of pars prostatica. Sinus-sac weakly developed and small. Ovary four ovoid lobes. Seminal receptacle large; oval; immediately posterior to ovary. Vitellarium originates between ovary and seminal receptacle; consists of seven main radial lobes which are finely divided to form about forty fairly short, tubular lobes. Excretory arms united in forebody.

TYPE-SPECIES. *Macradena perfecta* Linton, 1910 [by original designation].

MONORCHIMACRADENA Nahhas & Cable, 1964

Cyclocoel not reported. Testis single; immediately pre-ovarian. Seminal vesicle sac-like; immediately pre-testicular. Pars prostatica and ejaculatory duct about equal in length. Sinus-sac spherical to pyriform; small. Ovary oval. Seminal receptacle as large or larger than ovary; dorsal to ovary. Vitellarium seven digitiform or slightly branched lobes; united centrally; post-testicular. Excretory arms united in forebody.

TYPE-SPECIES. *Monorchimacradena acanthuri* Nahhas & Cable, 1964 [by original designation].

NEODICHADENA Yamaguti, 1971

Cyclocoel not reported. Testes oblique; immediately pre-ovarian. Seminal vesicle sac-like (may have constriction). Pars prostatica long. Ejaculatory duct about half length of pars prostatica. Sinus-sac small; spherical. Ovary oval. Seminal receptacle large; lateral to ovary. Vitellarium about eight tear-shaped lobes; post-ovarian. Excretory arms united in forebody.

TYPE-SPECIES. *Neodichadena acanthuri* (Siddiqi & Cable, 1960) [by original designation].

PSEUDODICHADENA Yamaguti, 1971

Cyclocoel present. Testes small; tandem; at level of ovary. Seminal vesicle elliptical; dorsal at level of gonads. Pars prostatica long. Ejaculatory duct short. Sinus-sac oval. Ovary four-lobed. Seminal receptacle post-ovarian. Vitellarium seven tear-shaped lobes; antero-lateral to ovary. Excretory arms united in forebody.

TYPE-SPECIES. *Pseudodichadena lobata* Yamaguti, 1971 [syn. *Dichadena acuta* of Siddiqi & Cable, 1960, *nec* Linton, 1910] [by original designation].

Subfamily **PROLECITHINAE** Yamaguti, 1971

Folliovitellotrematinae Gupta & Sharma, 1972 (*sic*)

Body spindle-shaped. Ventral sucker large, prominent. Cyclocoel present. Testes two; diagonal to symmetrical; at level of or slightly posterior to ventral sucker. Seminal vesicle saccular; in forebody. Pars prostatica short; vesicular. Sinus-sac and permanent sinus-organ absent. Large, spherical genital atrium present with muscular walls forming sucker-like structure (it is possible that this structure is an hermaphroditic duct surrounded by the remains of a sinus-sac). Ovary three- to four-lobed; near posterior extremity; overlying cyclocoel. Blind seminal receptacle posterior to ovary; at posterior extremity of body. Uterus mainly anterior to gonads. Vitellarium seven rounded lobes; immediately pre-ovarian; close to testes. Excretory arms not united in forebody. Parasitic in intestine of marine teleosts (Belonidae).

PROLECITHA Manter, 1961

Lobatovitelliovarium Yamaguti, 1965
Follicovitellosum Gupta & Sharma, 1972

As subfamily.

TYPE-SPECIES. *Prolecitha obesa* Manter, 1961 [by original designation].

Subfamily **QUADRIFOLIOVARINAE** Yamaguti, 1970

Body elongate to spindle-shaped. Muscular ventro-lateral flange or flanges present immediately posterior to ventral sucker. Caeca usually terminate blindly, but cyclocoel may be present. Testes two; pre-ovarian. Seminal vesicle in hindbody; saccular, constricted into portions or tubular. Pars prostatica usually short; tubular; in hindbody. Ejaculatory duct long; may be lined with cuticular villi. Sinus-sac oval. Permanent sinus-organ absent. Genital atrium short or apparently absent. Ovary oval or four-lobed. Blind seminal receptacle normally large; anterior or antero-dorsal to ovary. Uterus reaches to post-ovarian region. Vitellarium seven post-ovarian, claviform or oval lobes, or two groups of six to seven digitiform lobes, one pre-ovarian and one post-ovarian. Excretory arms united in forebody. Parasitic in stomach or pyloric caeca of acanthurid marine teleosts.

COMMENT. This subfamily is morphologically similar to the Macradenininae, differing fundamentally only in the presence of muscular flanges just posterior to the ventral sucker and in the length of the pars prostatica. It is worth noting that all of the macradeninine and quadrifoliovariine genera are parasitic in acanthurid teleosts.

Key to Quadrifoliovariinae

1. A. Muscular ventro-lateral flange present on one side of body only; cyclocoel present . . . *UNILACINIA*
   B. Muscular ventro-lateral flanges symmetrical; cyclocoel absent 2
2. A. Ovary 4-lobed; vitelline lobes in 2 antero-posteriorly oriented groups . . . *QUADRIFOLIOVARIUM*
   B. Ovary oval; vitelline lobes in one group . . . . *BILACINIA*

QUADRIFOLIOVARIUM Yamaguti, 1965

Pair of muscular ventro-lateral flanges immediately posterior to ventral sucker. Cyclocoel not reported. Testes tandem. Seminal vesicle a wide, convoluted tube; narrowing anteriorly. Pars prostatica short. Ejaculatory duct two to three times length of pars prostatica. Hermaphroditic duct convoluted; may be everted to form temporary sinus-organ. Sinus-sac thin-walled; elliptical to oval. Ovary four-lobed. Vitellarium in two antero-posteriorly oriented rosette-like groups; one pre- and one post-ovarian; united by collecting duct; each group has six or seven digitiform lobes. Parasitic in stomach and pyloric caeca of marine teleosts (*Naso*).

TYPE-SPECIES. *Quadrifoliovarium pritchardae* Yamaguti, 1965 [by original designation].

BILACINIA Manter, 1969

Holacanthitrema Yamaguti, 1970

Pair of bilobed, muscular ventro-lateral flanges; symmetrical; immediately posterior to ventral sucker. Cyclocoel not reported. Testes tandem to oblique. Seminal vesicle convoluted, wide and tubular or divided into four to five portions. Pars prostatica sigmoid. Ejaculatory duct one quarter to nearly equal length of pars prostatica. Hermaphroditic duct wide; straight. Sinus-sac oval; thin-walled. Ovary oval. Vitellarium seven rounded to claviform lobes; immediately post-ovarian. Parasitic in stomach and pyloric caeca of marine teleosts (*Naso* and *Holacanthus*).

Type-species. *Bilacinia australis* Manter, 1969 [by original designation].

UNILACINIA Manter, 1969

Bilobed muscular flange lateral to ventral sucker, on one side only. Cyclocoel present. Testes oblique. Seminal vesicle saccular; antero-dorsal to anterior testis. Ejaculatory duct twice length of pars prostatica. Hermaphroditic duct wide. Sinus-sac broadly ovoid. Ovary oval. Vitellarium seven short, digitiform lobes; postero-ventral to ovary. Parasitic in stomach of marine teleosts (*Naso*).

Type-species. *Unilacinia asymmetrica* Manter, 1969 [by original designation].

Subfamily **TRIFOLIOVARIINAE** Yamaguti, 1958

Body cylindrical; long and thin, fusiform or elongate oval. Ventral sucker present well inside anterior half of body. Gut-caeca terminate blindly; often wide. Testes two; pre-ovarian in anterior hindbody; separated from ovary by many loops of uterus. Seminal vesicle in forebody, at level of ventral sucker or in hindbody; tubular, moniliform or elongate oval. Pars prostatica short; tubular or vesicular. Ejaculatory duct short; enters hermaphroditic duct, which is continuation of uterus, laterally. Sinus-sac present surrounding hermaphroditic duct; weak and membranous; tubular or oval. Permanent sinus-organ absent. Genital atrium absent or small. Female reproductive complex close to posterior extremity. Ovary four-lobed. Laurer's canal present or absent. Seminal receptacle large; blind or canalicular; dorsal or antero-dorsal to ovary. Uterine seminal receptacle and Juel's organ absent. Uterus entirely or almost entirely pre-ovarian; coils confined to hindbody. Eggs without filaments. Vitellarium seven or eight claviform or digitiform lobes, which may be bilobed or irregularly branched distally; at level of ovary or immediately post-ovarian. Excretory arms united in forebody. Parasitic in intestine of marine teleosts.

Key to Trifoliovariinae

1. A. Body long and thin; seminal vesicle in hindbody or dorsal (to antero-dorsal) to ventral sucker, elongate oval (to tubular and sinuous); vitelline lobes claviform, unbranched, in rosette arrangement; Laurer's canal present . . . . . *TRIFOLIOVARIUM*
B. Body elongate oval to fusiform; seminal vesicle in forebody or antero-dorsal to ventral sucker, tubular, moniliform or elongate oval; Laurer's canal absent [or at least not reported] 2
2. A. Seminal vesicle elongate oval; vitellarium a rosette of 12 to 16 lobes (possible ca. 7 bilobed lobes); pars prostatica vesicular . . . . *PSEUDOLECITHASTER*
B. Seminal vesicle tubular or moniliform 3
3. A. Uterus mainly intercaecal; vitellarium 2 groups of 4 unbranched posteriorly oriented tubular lobes; seminal vesicle moniliform, antero-dorsal to ventral sucker . *ASSITREMA*
B. Uterus reaches extracaecally; vitellarium a rosette arrangement of 7 short tubular distally branched lobes; seminal vesicle tubular, in forebody . . *CLADOLECITHOTREMA*

TRIFOLIOVARIUM Yamaguti, 1940 [T(w)]

Body long and thin. Oral sucker funnel-shaped. Testes tandem to oblique; widely separated. Seminal vesicle elongate oval (or tubular and sinuous); in hindbody or dorsal to ventral sucker (or antero-dorsal to ventral sucker); connected to pars prostatica by short, aglandular duct. Pars prostatica tubular. Sinus-sac tubular. Laurer's canal present, uniting canalicular seminal receptacle with dorsal surface. Vitellarium seven claviform lobes at level of ovary.

TYPE-SPECIES. *Trifoliovarium acanthocepolae* Yamaguti, 1940 [by original designation].

COMMENT. Yamaguti (1940) originally described the ovary as being three-lobed; hence the generic name, but later (1971) corrected this observation to four-lobed. Having examined the type-material of *T. acanthocepolae*, we can confirm this emendation.

The information given above in parentheses is taken from the descriptions of *T. triacanthi* Bilqees, 1973, and *T. triacanthusi* Gupta & Ahmad, 1976. These species, which are probably synonymous, were described from *Triacanthus* spp. off the Indian sub-continent.

ASSITREMA Parukhin, 1976

Body small; oval to elongate oval. Gut-caeca wide. Testes symmetrical; separated by coils of uterus. Seminal vesicle short, moniliform; winding antero-dorsally to ventral sucker. Pars prostatica tubular (but wider in middle according to figure). Sinus-sac small; oval. Laurer's canal (?). Seminal receptacle (? blind or canalicular) present. Uterus almost entirely pre-ovarian; mainly inter-caecal. Eggs small. Vitellarium two symmetrical groups of four postero-laterally oriented, digitiform lobes; centre of each group immediately post-ovarian. Excretory arms (?).

TYPE-SPECIES. *Assitrema eichleri* Parukhin, 1976 [by original designation].

COMMENT. Parukhin's (1976c) figure indicates that the hermaphroditic duct is a continuation of the ejaculatory duct. In the other three genera of this subfamily the hermaphroditic duct is a continuation of the metraterm. This may be just a matter of interpretation, for there is no evidence that Parukhin sectioned either of his two specimens. There is a possibility, if the two specimens of *Assitrema* were young, that some of the differences between this genus and *Cladolecithotrema* are the result of age. This question cannot be resolved until further material of *Assitrema* is studied.

CLADOLECITHOTREMA Ichihara, 1970 [T(w,s)]

Body elongate oval. Gut-caeca wide. Testes oblique; widely separated. Seminal vesicle tubular; convoluted in forebody. Pars prostatica tubular. Sinus-sac small; oval. Laurer's canal absent. Blind seminal receptacle present. Uterine field reaches extra-caecally. Vitellarium a rosette arrangement of seven digitiform, distally branched lobes; centre immediately post-ovarian.

TYPE-SPECIES. *Cladolecithotrema callionymi* Ichihara, 1970 [by original designation].

COMMENT. We do not agree with Gupta & Sharma's (1975) proposed synonymy of *Cladolecithotrema* and *Trifoliovarium*. We consider that the shape and position of the seminal vesicle, the shape of the vitellarium and the absence or presence of Laurer's canal are sufficient criteria to distinguish these taxa.

PSEUDOLECITHASTER Campbell & Munroe, 1977

Body fusiform. Testes symmetrical; separated by coils of uterus. Seminal vesicle elongate oval; in forebody; connected to pars prostatica by short aglandular duct. Pars prostatica vesicular. Sinus-sac small; elongate oval. Ovary 'several irregular lobes' (four visible in figure). Laurer's canal (?). Seminal receptacle (?). Vitellarium a rosette of twelve to sixteen lobes (figure suggests ca. seven bilobed lobes); at level of ovary.

TYPE-SPECIES. *Pseudolecithaster antimorae* Campbell & Munroe, 1977 [by original designation].

Family **PTYCHOGONIMIDAE** Dollfus, 1937

Body medium sized; oval. Ecsoma absent. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; oral sucker larger than ventral sucker; latter situated in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' absent. Gut-caeca form uroproct. Testes two; post-ovarian; tandem; in middle of hindbody. Seminal vesicle dilate, tubular; thin-walled; extending posteriorly into anterior hindbody. Pars prostatica tubular. Ejaculatory and hermaphroditic duct short. Permanent sinus-organ a small cone. Sinus-sac absent. Genital atrium contains three distinct concentric folds in its wall which surround sinus-organ. Genital pore mid-ventral in forebody. Ovary oval; pre-testicular in hindbody. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterine field extends between level posterior to testes and ventral sucker. Eggs numerous; without filaments. Vitellarium follicular; occurs in lateral fields extending throughout most of hindbody. Excretory vesicle Y-shaped; arms unite twice in forebody. Parasitic in stomach of elasmobranchs (normally carchariniform sharks).

PTYCHOGONIMUS Lühe, 1900 [t(w,s)]

Defined as family.

TYPE-SPECIES. *Ptychogonimus megastoma* (Rudolphi, 1819) [by monotypy].

COMMENT. The above definition does not take into account the description of '*Ptychogonimus megastoma*' given by Vigueras (1956), which differs from other descriptions markedly and requires confirmation.

We have examined one type-specimen (whole-mount) of *Ptychogonimus fontanus* Lyster, 1939, and consider that, although it is not in good condition, this specimen appears to be an azygiid, bearing a strong resemblance to contracted forms of *Azygia longa* (Leidy, 1851).

Family **SCLERODISTOMIDAE** Odhner, 1927

Prosogonotrematidae Vigueras, 1940
Bhaleraoiidae Srivastava, 1948
Mabiaramidae Teixeira de Freitas & Kohn, 1967

Body usually large; stout or elongate. Ecsoma absent. Body-surface smooth, but may be rugate. Oral and ventral suckers well developed; ventral sucker just posterior to middle, in middle or in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present or absent. Gut-caeca terminate blindly close to posterior extremity. Testes two; symmetrical, oblique or in tandem; pre-ovarian; in forebody, dorsal to ventral sucker or in anterior hindbody. Seminal vesicle tubular; convoluted or winding in forebody. Pars prostatica tubular, occasionally with wide lumen; long; convoluted or not; external gland-cells may be delimited. Ejaculatory duct present; unites with metraterm within sinus-organ forming short hermaphroditic duct. Permanent sinus-organ usually well developed; conical to cylindrical. Sinus-sac well developed, weakly developed or apparently absent. Genital atrium well developed; often almost entirely filled by sinus-organ. Genital pore mid-ventral in forebody. Ovary globular to oval; well posterior to and usually separated from testes by loops of uterus; in posterior forebody, dorsal to ventral sucker or anterior to mid-hindbody. Mehlis' gland usually posterior or postero-lateral, occasionally antero-lateral, to ovary. Laurer's canal present; opens dorsally or into rudimentary Juel's organ. Rudimentary seminal receptacle present or absent. Canalicular or blind seminal receptacle absent. Uterine seminal receptacle present. Uterus mainly in either fore- or hindbody; mainly pre- or post-ovarian. Eggs small; numerous; non-filamented. Vitellarium four to seven convoluted, tubular branches, which may subdivide; either mainly pre- or post-ovarian; either mainly in fore- or hindbody. Excretory vesicle Y-shaped; stem relatively long; arms united in forebody. Manter's organ (accessory excretory vesicle) present; single or double; dorsal to stem of excretory vesicle. Parasitic in gut (mainly stomach) (?), occasionally in body-cavity, of marine teleosts.

COMMENT. Parukhin (1976b) erected a new subfamily, the Pseudosclerodistomoidinae, within this family for *Pseudosclerodistomoides kurotchkini*, a new genus and species from the gall-bladder of *Lethrinus miniatus* in the Indian Ocean. Several features of this species, such as the position of the testes and the genital pore and the nature of the seminal receptacle, suggest that it is not a hemiuroid.

Key to Sclerodistomidae

1. A. Manter's organ double; testes in anterior hindbody . . **SCLERODISTOMINAE** (p. 112)
B. Manter's organ single; testes in forebody 2
2. A. Ovary in forebody or at level of ventral sucker; uterus and vitellarium mainly pre-ovarian **PROSOGONOTREMATINAE** (p. 112)
B. Ovary in hindbody; uterus and vitellarium mainly post-ovarian . **PROSORCHIINAE** (p. 112)

Subfamily **SCLERODISTOMINAE** Odhner, 1927

Body stout. Ventral sucker near middle of body. 'Drüsenmagen' present. Testes symmetrical to oblique; in anterior hindbody. Pars prostatica long and convoluted. Sinus-sac distinctly present; musculature diffuse; surrounding base of genital atrium. Sinus-organ a stout cone. Ovary near or just anterior to middle of hindbody. Laurer's canal opens dorsally. Rudimentary seminal receptacle present. Uterus almost entirely in hindbody; mainly posterior to gonads, reaching near to posterior extremity. Vitellarium composed of convoluted, tightly helical, unbranched, filamentous tubules; commonly arranged with three on one side of body, four on other; present laterally in post-testicular region of hindbody. Manter's organ (accessory excretory vesicle) double; symmetrical. Parasitic in stomach and (?) body-cavity of marine teleosts.

SCLERODISTOMUM Looss, 1912 [t(w,s); n(w)]

Mabiarama Teixeira de Freitas & Kohn, 1967

Defined as subfamily.

TYPE-SPECIES. *Sclerodistomum italicum* (Stossich, 1893) [by monotypy].

Subfamily **PROSOGONOTREMATINAE** Vigueras, 1940

Body stout. Ventral sucker in middle or just posterior to middle of body. 'Drüsenmagen' absent. Testes symmetrical; in forebody. Pars prostatica long and sinuous or convoluted. Sinus-sac well developed, but composed of diffuse musculature. Sinus-organ conical to cylindrical. Ovary in forebody or at level of ventral sucker. Laurer's canal short; opens into large rudimentary Juel's organ; dilated proximally forming small rudimentary seminal receptacle. Rudimentary Juel's organ post-ovarian [distinct in sections]. Uterus mainly pre-ovarian; does not extend into hindbody. Vitellarium about three (two to four) convoluted, tubular branches on each side of body, which may subsequently divide; mainly pre-ovarian in forebody. Manter's organ (accessory excretory vesicle) single; median. Parasitic mainly in stomach of marine teleosts.

PROSOGONOTREMA Vigueras, 1940 [t(w,s)]

(?) *Bhaleraoia* Srivastava, 1948

Defined as subfamily.

TYPE-SPECIES. *Prosogonotrema bilabiatum* Vigueras, 1940 [by monotypy].

COMMENT. Nasir (1973) considers this genus to be monotypic, synonymizing seven other species with *P. bilabiatum*. We have included *Bhaleraoia* Srivastava, 1948, as a questionable synonym of this genus, because, although similar in gross morphology, it is poorly described and purported to possess a uroproct.

Subfamily **PROSORCHIINAE** Yamaguti, 1934

Body elongate oval to elongate. Ventral sucker normally within anterior half of body, but occasionally in middle. 'Drüsenmagen' absent. Testes tandem to almost symmetrical; in forebody or dorsal to ventral sucker. Pars prostatica broad; usually straight or arcuate; lumen wide;

external gland-cells delimited. Sinus-sac apparently absent or (?) weakly developed. Sinus-organ conical to cylindrical. Ovary in hindbody. Laurer's canal long and opening into rudimentary Juel's organ or short and opening to exterior on dorsal surface; may or may not be dilate proximally forming rudimentary seminal receptacle. Uterus mainly post-ovarian in hindbody. Vitellarium two to four branching or seven convoluted and filamentous tubules; mainly post-ovarian in hindbody; reaching near to posterior extremity. Manter's organ (accessory excretory vesicle) single; median.

Key to Prosorchiinae

1. A. Laurer's canal long, opening into rudimentary Juel's organ, dilated proximally forming rudimentary seminal receptacle . . . . ***PROSORCHIS***
B. Laurer's canal short, opening·dorsally to exterior; rudimentary seminal receptacle absent ***PROSORCHIOPSIS***

COMMENT. These two closely related genera essentially appear to differ only in the nature of Laurer's canal. As few authors appear to have sectioned their material, many of the descriptions in the literature must be used with some degree of caution. Nevertheless, both from the literature and from our own sectioned material of *Prosorchiopsis*, it is evident that two distinct forms of Laurer's canal appear to be present.

PROSORCHIS Yamaguti, 1934

Laurer's canal long; opens distally into well-developed rudimentary Juel's organ ('terminal vesicle'); dilate proximally forming rudimentary seminal receptacle.

TYPE-SPECIES. *Prosorchis psenopsis* Yamaguti, 1934 [by original designation].

COMMENT. The presence of a 'terminal vesicle' at the distal extremity of Laurer's canal has been reported in a number of descriptions of species from this genus. Considering the nature of these descriptions, especially that of Yamaguti (1934), and the structure of the related *Prosogonotrema*, we have interpreted this 'terminal vesicle' as being a rudimentary Juel's organ.

PROSORCHIOPSIS Dollfus, 1947 [t(w,s)]

Laurer's canal short; opening dorsally to exterior; distal region may be slightly dilate and possess glandular wall; rudimentary seminal receptacle absent.

TYPE-SPECIES. *Prosorchiopsis legendrei* Dollfus, 1947 [by original designation].

COMMENT. In sectioned material, part of the distal region of Laurer's canal was slightly dilate and possessed a diffuse, glandular wall (see Gibson & Bray, 1977). It is possible that this represents an early stage in the development of a rudimentary Juel's organ.

It should be pointed out that a uterine seminal receptacle was not present in our sectioned material, and its presence or absence could not be ascertained either from the literature or from whole-mounts. Considering that there is no alternative seminal storage apparatus and that it is present in *Prosorchis*, we can only assume that it is normally present in *Prosorchiopsis*.

Addendum to Sclerodistomidae

It is possible that *Eurycoelum* Brock, 1886, and *Distoma gigas* Nardo, 1827, two forms not recorded since the nineteenth century, are also sclerodistomids; but the descriptions of these taxa are incomplete. *Eurycoelum sluiteri* was described (Brock, 1886) from the stomach of *Lutjanus sanguineus* [=*Diacope metallicus*] off Java. The genus has been considered by certain workers, including Yamaguti (1971), to be a synonym of *Hemiurus*; but this is not the case. In fact it is possible that this genus may be a synonym of *Prosogonotrema*, which has been recorded from *Lutjanus* spp. on several occasions; but only an examination of the type-specimens, which we have been unable to trace, or material from the type-host and locality can substantiate this. The situation with regard to *Distoma gigas*, a gigantic species from the stomach of *Luvarus imperialis*, has been discussed in detail by Gibson & Bray (1977).

SCLERODISTOMOIDIDAE fam. nov.

Body large; stout, elongate oval and attenuated anteriorly. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed, small; ventral sucker well inside anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present. Gut-caeca sinuous; end blindly near posterior extremity, very close to stem of excretory vesicle (no union observed). Testes two; slightly lobate; symmetrical to oblique; in hindbody close to ventral sucker; pre-ovarian. Seminal vesicle tubular convoluted in forebody. Pars prostatica short; tubular with wide lumen. Ejaculatory duct short. Hermaphroditic duct short; present within small, cone-shaped permanent sinus-organ. Sinus-sac small and poorly developed or apparently absent. Genital atrium well developed. Genital pore mid-ventral at level of pharynx. Ovary oval; in middle of body; separated from testes by loops of uterus. Mehlis' gland postero-lateral to ovary. Laurer's canal and uterine seminal receptacle present. Canalicular or blind seminal receptacle and Juel's organ absent. Uterus inter-caecal; coiled almost entirely in hindbody, in both pre- and post-ovarian fields; with narrow, convoluted descending loop reaching near to posterior extremity and convoluted ascending loop which is initially narrow and then much broader. Eggs small; numerous; without filaments. Vitellarium tubular; with two main collecting ducts situated medially, one anteriorly and other posteriorly oriented; laterally directed dendritic branches present between testes and level a short distance anterior to posterior extremity. Excretory vesicle Y-shaped; stem short; arms initially in dorsal and ventral fields, pass laterally and unite in forebody. Parasitic in gall-bladder of marine teleosts.

COMMENT. We have erected a new family for the genus *Sclerodistomoides* Kamegai, 1971, because it differs significantly from the accacoeliids in the structure of the pharynx, from the sclerodistomids in the absence of Manter's organ, and from both groups in the unique orientation of the main collecting ducts of the vitelline system. Its closest relative appears to be the accacoeliid genus *Paraccacladium*.

SCLERODISTOMOIDES Kamegai, 1971 [T(w); t(s)]

Defined as family.

TYPE-SPECIES. *Sclerodistomoides pacificus* Kamegai, 1971 [by original designation].

COMMENT. *Lintonius novikovi* Baeva, 1965, does bear some superficial resemblance to *Sclerodistomoides*, but the description of this species by Baeva (1965) does not include enough data to confirm this. Yamaguti (1971) suggested that it might be a sclerodistomid.

Family **SYNCOELIIDAE** Looss, 1899

Body elongate or dorso-ventrally flattened; usually with pedunculate ventral sucker. Ecsoma absent. Body-surface smooth, but commonly papillate on forebody and on peduncle, if present. Oral and ventral suckers well developed; may possess accessory suckers around their rim. Glandular cells common in subtegumentary parenchyma and within musculature of suckers. Pharynx well developed. Oesophagus short. Cyclocoel usually present, but gut-caeca may end blindly (?) or form a uroproct. Testes eleven to eighteen distinct, oval follicles (usually arranged in pairs), seven to eight transverse rows of small follicles, or just a large number of irregular follicles; pre-ovarian, in hindbody. Seminal vesicle thin-walled; tubular; winding or sinuous; in forebody. Pars prostatica tubular. Ejaculatory duct short. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Permanent sinus-organ and sinus-sac present or absent. Genital pore mid-ventral in anterior forebody. Ovary post-testicular; composed of five large, oval, isolated lobes or numerous irregular follicles. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent, but rudimentary seminal receptacle may be present. Uterus passes posteriorly but coils mainly in pre-ovarian hindbody. Eggs numerous, small, non-filamented. Vitellarium usually seven (occasionally five or six) isolated, oval lobes, or irregular acinous bunches or rows of follicles; post-ovarian. Excretory vesicle Y-shaped; arms united in forebody, may initially run in dorsal and ventral fields. Free floating metacercarial stage present. Parasitic in branchial and buccal cavities, on skin, in (?) oviduct and in (?) gut of elasmobranchs and marine teleosts.

Key to Syncoeliidae

1. A. Ovary numerous irregular follicles arranged in rows; vitellarium irregular acinous bunches or rows of follicles . . . . . . **OTIOTREMATINAE** (p. 115)
   B. Ovary 5 large isolated lobes; vitellarium 5 to 7 oval, isolated lobes . **SYNCOELIINAE** (p. 116)

Subfamily **SYNCOELIINAE** Looss, 1899

Small accessory suckers around rim of suckers absent. Peduncle usually present. Cyclocoel present. Testes eleven to eighteen distinct, oval lobes; usually arranged in pairs. Permanent sinus-organ present or absent. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Sinus-sac absent or rudimentary. Ovary composed of five large, isolated follicles. Rudimentary seminal receptacle may be present as proximal dilation of Laurer's canal. Uterus arranged in large, regular loops dorsally and ventrally to gonads. Vitellarium seven (occasionally five or six) small, isolated, oval lobes. Parasitic in branchial and buccal cavities (? with occasional records from gut) of sharks and marine teleosts.

COMMENT. Our work with this group indicates that *Syncoelium* Looss, 1899, can be conveniently split into two distinct genera on the basis of the presence or absence of a sinus-organ (Gibson & Bray, 1977). When present, the sinus-organ is a well-developed structure, visible in sections and whole-mounts in both adults and metacercariae (see Gibson, 1976). In addition, in forms lacking a sinus-organ the genital atrium appears to be indistinguishable from the hermaphroditic duct, the hindbody tends to be spatulate rather than tubular, and the ventral sucker is somewhat less pedunculate. Furthermore, the latter forms have been recorded from the gills, whereas the forms possessing a sinus-organ usually occur in the buccal cavity and on the gill-arches.

Key to Syncoeliinae

1. A. Permanent sinus-organ absent; hermaphroditic duct indistinguishable from genital atrium; tendency for hindbody to be spatulate; ventral sucker normally sessile or on short peduncle; normally parasitic on gills . . . . *SYNCOELIUM*
   B. Permanent sinus-organ present; hermaphroditic duct easily distinguishable from genital atrium; hindbody usually tubular; ventral sucker usually on well-developed peduncle; usually parasitic in buccal cavity or on gill-arches . . . . . . *COPIATESTES*

SYNCOELIUM Looss, 1899

Hindbody broad or spatulate. Ventral sucker sessile or surmounted on short peduncle. Permanent sinus-organ absent. Hermaphroditic duct indistinguishable from genital atrium. Parasitic on gills (? and in intestine) of sharks and marine teleosts.

TYPE-SPECIES. *Syncoelium ragazzii* (Setti, 1897) [by monotypy].

*COPIATESTES** Crowcroft, 1948 [n(w,s)]

Hindbody elongate, tubular. Ventral sucker surmounted on well-developed peduncle. Permanent sinus-organ present. Hermaphroditic duct and genital atrium easily distinguishable. Parasitic in branchial (especially gill-arches and gill-rakers) and buccal cavities (? and intestine) of marine teleosts.

---

* It is also spelt *Capiatestes* in original publication, but this is a typographical error.

TYPE-SPECIES. *Copiatestes thyrsitae* Crowcroft, 1948 [by original designation].

Subfamily OTIOTREMATINAE Skrjabin & Guschanskaja, 1957

Paronatrematinae Skrjabin & Guschanskaja, 1957 [proposed, but not named, by Dollfus (1950)].

[*Paronatrema* is poorly known.] Accessory suckers may be present around rim of suckers. Cyclocoel present (? or absent; caeca may end blindly or form uroproct). Testes numerous irregular follicles or seven to eight irregular transverse rows of follicles. Hermaphroditic duct present within sinus-sac (? not clearly described in *Paronatrema*). Permanent sinus-organ absent. Ovary composed of numerous irregular follicles which may be arranged in rows. Vitellarium irregular acinous bunches or rows of follicles. Parasitic in branchial cavity or on skin (? or in oviduct or intestine) of sharks and rays.

Key to Otiotrematinae

1. A. Small accessory suckers present on oral sucker and/or ventral sucker . ***PARONATREMA***
   B. Small accessory suckers on suckers absent (papillae present within oral sucker) ***OTIOTREMA***

OTIOTREMA Setti, 1897 [t(w,s)]

Forebody cylindrical; hindbody flattened, alate, recurved. Papillae present within oral sucker; small accessory suckers within suckers absent; ventral sucker pedunculate. Gut-caeca sinuous in forebody; with numerous diverticulate outgrowths in hindbody; forming cyclocoel. Sinus-sac large, reaching close to dorsal surface. Ovary and vitellarium consisting of numerous acinous bunches of follicles, posterior to numerous follicular testes. Uterus in transverse coils; present in lateral fields of hindbody. Parasitic in branchial cavity (? or intestine) of sharks.

TYPE-SPECIES. *Otiotrema torosum* Setti, 1897 [by original designation].

COMMENT. We have examined some of the material collected by Looss, and it appears to agree well with his description (Looss, 1899).

PARONATREMA Dollfus, 1937 [t(w); n(w)]

[This genus is poorly known.] Forebody sub-cylindrical; hindbody flattened, oval. Small accessory suckers present within oral and/or ventral suckers; ventral sucker large, but apparently not pedunculate. Gut-caeca sinuous; apparently end blindly (? or form uroproct or cyclocoel: interpretations uncertain). Testes consist of rows of follicles or segmented tubules. Ovary composed of irregular follicles (interpretations conflict). Vitellarium consists of rows of follicles or segmented tubules. Uterus numerous transverse coils in hindbody. Parasitic on skin or (?) in oviduct or stomach of sharks and rays.

TYPE-SPECIES. *Paronatrema vaginicola* Dollfus, 1937 [by monotypy].

COMMENT. It would appear that in some descriptions the ovary and Mehlis' gland may have been confused.

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IV. A discussion on the evolution of the Hemiuroidea

Evolutionary trends in the Hemiuroidea

The presentation of any evolutionary picture for the Platyhelminthes must remain hypothetical, as it is unlikely that there will ever be any fossil record due to the soft-bodied nature of these animals. Possible evolutionary patterns can only be exposed by the knitting together of general morphological trends in organs, organ-systems and whole animals. Having distinguished a trend, there is the problem of deciding which way the trend is moving, and hence which is the primitive and which is the advanced condition. In addition, the possibility should not be forgotten that an intermediate form is primitive and that evolution is proceeding in two opposite directions. In order to assess which form is primitive, it is helpful to adopt the use of certain external indicators. As far as parasitic helminths are concerned useful indicators include:

1. *The supposed 'primitiveness' of the host*

   Although superficially it appears more likely that the more archaic and primitive vertebrates harbour more archaic and primitive parasites, this is not necessarily so. Owing to the variable ecological factors involved, archaic hosts can harbour what appear to be 'advanced' parasites, and *vice versa.* In addition, there are often widely differing opinions as to the relative ages of certain groups of vertebrates, and this tends to limit its value as an indicator. One might expect, however, that a group of helminths restricted to birds would be more advanced than one restricted to elasmobranchs. Unfortunately, the vast majority of the hemiuroids are parasitic in fishes, and, although certain primitive groups are recognized, it is not known for certain whether elasmobranchs are more primitive than bony fishes (Osteichthyes).

Amongst the hemiuroids only the azygiids appear to occur in fishes which are widely held to be primitive. *Otodistomum* commonly occurs in the shark *Hexanchus* and has been recorded from *Chlamydoselachus* and *Heterodontus*, and both *Azygia* and *Leuceruthrus* occur in the holostean *Amia.* Other groups occuring in elasmobranchs are the ptychogonimids and the syncoeliids, the Ptychogonimidae and the Otiotrematinae being entirely restricted to these hosts. *Azygia* has also been recorded from *Acipenser*, a member of primitive group Chondrostei; but little emphasis can be placed upon this result as *Derogenes* and several species of hemiurid have also been recorded from this host. This apparent mixture of what we believe to be 'primitive' and relatively 'advanced' forms is possibly associated with the migratory habit of sturgeons and the low degree of host-specificity exhibited by some of the more 'advanced' hemiuroids. There is also a single record of *Halipegus* from the related chondrostean *Polyodon.* Except for certain halipegine derogenids, which occur in amphibians and, rarely, in amphibious snakes, and the pulmovermine hemiurids, which are restricted to the lungs of sea-snakes, the remainder of the hemiuroids occur in teleosts.

2. *The habitat of the host*
   Parasites of aquatic vertebrates will tend to be more primitive than those from terrestrial vertebrates, because aquatic vertebrates tend to be more primitive than terrestrial vertebrates and because it is much easier to envisage the origins of parasitic platyhelminths in aquatic conditions. All the hemiuroids are parasitic in aquatic or amphibious hosts, the majority being parasitic in marine teleosts, but a few groups are commonly found in freshwater hosts. Unfortunately, there is no conclusive evidence to suggest that teleosts arose in freshwater, or *vice versa*, although a freshwater origin is preferred by some workers. It should be emphasized that any evidence based upon the habitat of the host should be treated with caution, as various hosts may have passed from fresh- to salt-water or from water to land, and back, on more than one occasion during the course of their evolution.

Amongst the hemiuroids, only the azygiids and the halipegine derogenids are successful parasites of freshwater fishes, and only the isoparorchiids, a very small group, are restricted to these hosts. One interesting coincidence is that all three of the azygiid genera from freshwater fishes occur in North America, two being endemic, and that this is the only region of the world where holostean fishes survive. Another possible coincidence is that the majority of halipegine genera and the majority of isoparorchiid records occur in Asia, especially in the southern half of the continent: this location is the possible centre of evolution and radial dispersion of freshwater teleosts (see Darlington, 1957).

3. *Host-specificity*
   One might expect helminths with a high-degree of host-specificity to be more primitive than those with a low-degree. This is because it is likely that highly specific associations develop over a long period of time, and once they have arisen the further evolution of the parasite itself tends to be restricted to within the limits of the evolution of the host. This is a very general feature, however, and as digeneans tend to have a low degree of host-specificity with regard to their vertebrate host, it is of limited value.

It is worth noting, nevertheless, that the host-range of the adult forms of certain groups and genera do tend to be restricted. The accacoeliines, with the exception of *Tetrochetus*, occur only in molid teleosts and the ptychogonimids appear to be entirely or almost entirely restricted to galeomorph sharks. *Bathycotyle* and *Hirudinella* parasitize scombroid and coryphaenid teleosts, and *Botulus* and *Lampritrema* are usually restricted to *Alepisaurus* and *Lampris*, respectively. Prominent among other examples are the macradeninine and quadrifoliovariine lecithasterids, which occur only in acanthurid teleosts. Alternatively, many members of the Hemiuridae, Lecithasteridae, Bunocotylidae and Derogenidae appear to exhibit little or no host specificity amongst marine teleosts, although certain individual species or genera may appear to be highly host-specific. One species of *Halipegus* is reported to occur in freshwater teleosts and amphibians. The azygiids are present in freshwater teleosts, elasmobranchs, holosteans and rarely in chondrosteans, and although they appear to be restricted to certain groups of elasmobranchs, they appear to exhibit little host-specificity.

It is obvious in many of the above cases, e.g. the accacoeliines, that much of the apparent host-specificity is ecological rather than immunological or physiological, and it is likely that ecologically based host-specificity has less evolutionary significance, as it would appear that an ecological restriction is a prerequisite for the development of other types of host-specificity. Our lack of knowledge of the life-history in many cases, however, prohibits the differentiation of these types. Nevertheless, the above examples do tend to illustrate the fact that there is a tendency for the successful groups, such as derogenids, hemiurids, lecithasterids and bunocotylids to exhibit in general a low degree of host-specificity, while the smaller groups, such as accacoeliids, hirudinellids, ptychogonimids, etc. tend to be more restricted. If our hypothesis that host-specificity is acquired over a long period of association is correct, then it is likely that these smaller groups will tend to be more primitive than the larger. The azygiids occupy an anomalous position in that to some extent they are restricted to particular groups of fishes, but within these groups they are widespread. This might be explained by the fact that they are a small, but successful, group which occupy niches, i.e. the stomach of freshwater fishes and elasmobranchs, where competition from other digeneans is severely limited.

4. *Related groups*

   Undoubtedly the most important evidence can be taken from features common in groups which are held to be related to, and perhaps more primitive than, the group under study. Digeneans, monogeneans, cestodes and aspidogastreans are generally thought to have evolved from primitive rhabdocoel turbellarians, possibly similar to the Dalyellida, which may inhabit the mantle-cavity or viscera of bivalves. Most authorities now agree that the Aspidogastrea is the closest relative of the Digenea, and Rohde (1971a) in an abstract states: 'The Aspidogastrea are considered to be primitive, direct decendents of turbellarians, which are not yet closely adapted to parasitism and have not yet incorporated the vertebrate host as a fixed component in their life-cycle. They are closely related to the ancestors of the Digenea. Aspidogastrea and Digenea are both primarily parasites of molluscs.' In the same context Rohde (1971b) refers to the Aspidogastrea as 'living fossils'. It is likely, therefore, that features common to the Aspidogastrea and Digenea either must be primitive or are features produced by parallel or convergent evolution. Some primitive features may also be common in other parasitic platyhelminths and in the rhabdocoels; but, since these groups are successful, widely specialized and more distantly related, great care should be taken in the interpretation of any correlations, as the same features have undoubtedly been evolved independently by parallel and convergent evolution. Beklemishev (1964 [1969]), for example, states, when discussing the reproductive system of the Platyhelminthes: 'In spite of the great diversity of these adaptations, which appear independently in the various groups, the problems involved are repeatedly solved by similar methods, and that in animals far apart in the system.'

When attempting to decide which of a group is primitive, one must, therefore, look for a succession of trends which tend to flow in the same direction. It is unlikely, however, that one will encounter all of the trends proceeding 'satisfactorily' in the same animal. It is a fact that parallel and convergent evolution do occur, and each species is adapted to its particular niche rather than to illustrate an evolutionary picture. Parallel evolution is important because, as the members of the group originally shared the same gene-pool, the same mutations are likely to occur down the separate evolutionary branches, and thus the same features may evolve independently in several different sub-groups. It is essential, therefore, that one looks at the overall trends in the group as a whole. This is especially important where the loss of organs may have occurred.

In an attempt to show the evolutionary trends within the Hemiuroidea, we have followed three different organs and organ-systems in which definite trends do occur. These are: (1) the seminal storage and disposal apparatus in the female reproductive system; (2) the vitellarium; and (3) the terminal genitalia.

(1) *Seminal storage and disposal apparatus in the female reproductive system.* One of the most significant, but not one of the most obvious, trends in the Hemiuroidea is the development of the seminal storage and disposal apparatus, especially the latter, in the female system. In the majority of hemiuroids the proximal region of the uterus forms a seminal reservoir and is termed the *uterine seminal receptacle*. As a uterine seminal receptacle occurs in the Aspidogastrea (see Rohde, 1971a), it is likely that this condition is primitive in digeneans. Evidence from other platyhelminth-groups is difficult to interpret as they are specialized and involve, in the case of the Turbellaria, a vagina (copulatory canal) and several different types of seminal receptacle, and, in the case of the Monogenea and Cestoda, usually a vagina (or vaginae) with a dilation which forms a seminal receptacle. However, in some rhabdocoel turbellarians such as *Mesostoma*, a seminal receptacle in the form of a dilation of the oviduct does occur. Considering that the ovo-vitelline canal, which is the equivalent of the uterus in the Digenea, is short and that there is no Mehlis' gland, this feature is somewhat similar to a uterine seminal receptacle.

As stated above, the sperm in the majority of hemiuroids is stored in the proximal region of the uterus. From the uterus small amounts of activated sperm pass through Mehlis' gland, where presumably fertilization of the ova usually occurs. Excess and spent sperm, plus excess vitelline material, are then disposed of via Laurer's canal, which in certain groups, e.g. the Azygiidae, Accacoeliidae and Hirudinellidae, connects the oviduct with the exterior via a dorsal pore (see Fig. 6; arrangement A). Such sperm and vitelline material in Laurer's canal can be seen in sectioned material: occasionally ova are also present. This process is naturally very wasteful, and it is apparent that certain turbellarians and monogeneans have developed an analogous duct, the genito-intestinal canal, which disposes of similar residues by transporting them into the gut, in order that this material can be re-processed. Our work has shown that some hemiuroids appear to have evolved a special organ, *Juel's organ*, within which this waste-material is degraded and re-absorbed. It is clear that this organ did not arise overnight, as traces of its development can be seen in present forms. In groups, such as Gonocercinae, Syncoeliinae and Isoparorchiidae, the proximal region of Laurer's canal is slightly dilated, forming a *rudimentary seminal receptacle*, within which excess spermatozoa and vitelline material are stored before passing along the remainder of the canal (see Fig. 6; arrangement B). Our observations suggest that the excess material is killed or stored until it dies, and that it may begin to disintegrate within the rudimentary seminal receptacle, before being passed along the canal. The distal part of the canal in these groups tends to be slightly glandular in nature, and the pore itself is often tightly closed by a sphincter: thus, it is possible that some re-absorption may occur in these distal regions. In forms such as *Derogenes* and apparently *Prosorchis*, a *rudimentary Juel's organ* is found (see Fig. 6; arrangement C). In these cases the Laurer's canal does not open to the exterior, as the distal part of the duct is modified and forms an oval structure with a similar amorphous appearance to that of a fully-developed Juel's organ. During the course of evolution, Laurer's canal has become shorter, thus bringing the rudimentary Juel's organ and rudimentary seminal receptacle closer together. In *Prosogonotrema* these two structures are very close together (Fig. 4B). This process has continued until the rudimentary Juel's organ completely envelopes the rudimentary seminal receptacle, thus forming a complete Juel's organ (see Fig. 6; arrangement D). The enclosed rudimentary seminal receptacle has been known in the past as the 'inner vesicle' (Juel, 1889; Lander, 1904). A complete Juel's organ has been observed in *Genarchopsis* (Anjaneyulu, 1968; Madhavi & Rao, 1974), *Elongoparorchis* (Madhavi & Rao, 1974), in numerous hemiurids, knowingly or unknowingly, by several authors, including Juel (1889) and Lander (1904), and by ourselves in various hemiurids, *Hysterolecitha* and *Arnola*. A final development, which appears to have occurred during the development of the Opisthadeninae, and

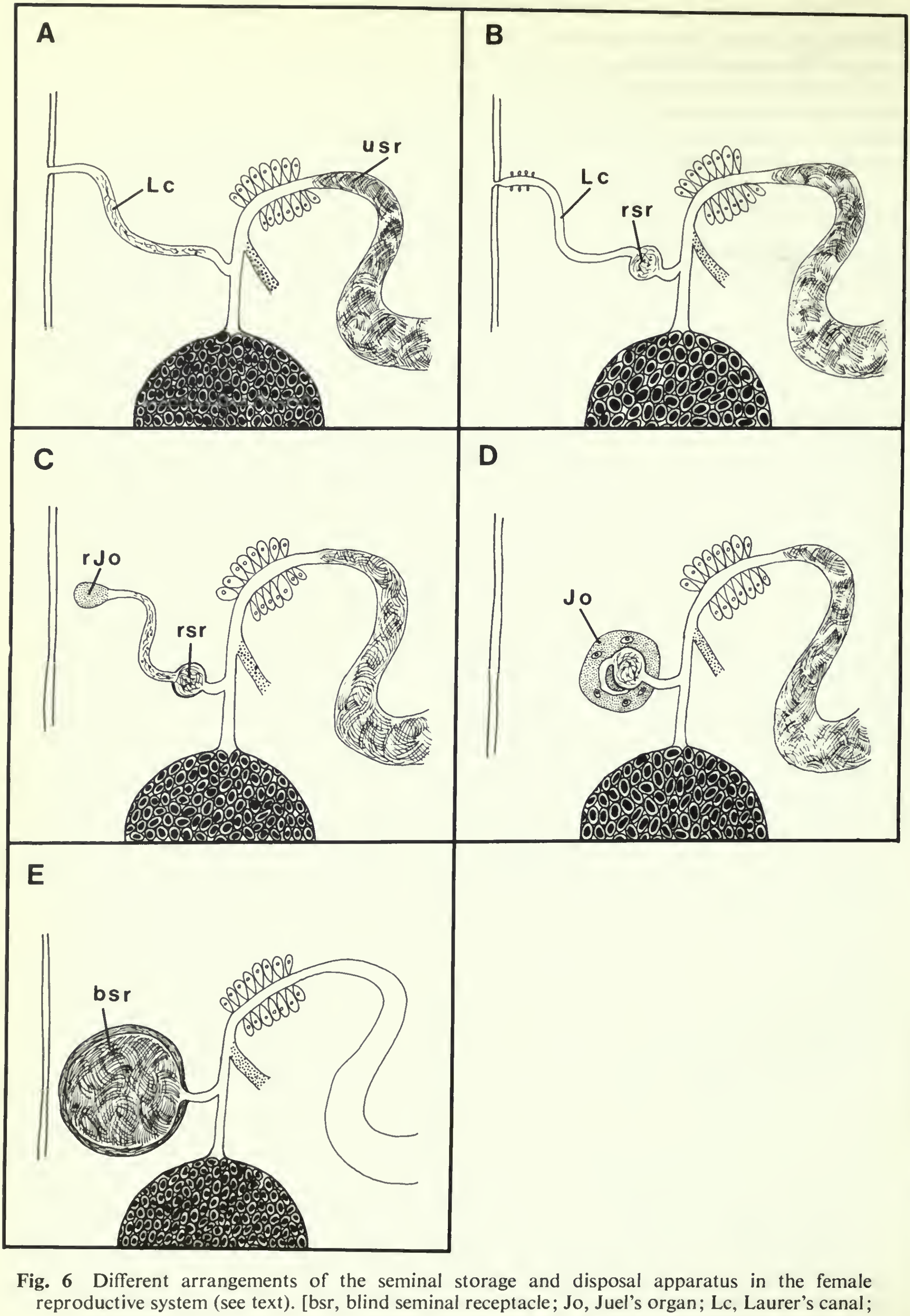
A
usr
Lc
B
Lc
rsr
C
rJo
rsr
D
Jo
E
bsr

Fig. 6 Different arrangements of the seminal storage and disposal apparatus in the female reproductive system (see text). [bsr, blind seminal receptacle; Jo, Juel's organ; Lc, Laurer's canal; rJo, rudimentary Juel's organ; rsr, rudimentary seminal receptacle; usr, uterine seminal receptacle.]

probably the majority of the lecithasterids, is that the inner vesicle expands to fill Juel's organ, thus forming a *blind seminal receptacle* (see Fig. 6; arrangement E). The uterine seminal receptacle is lost in these groups. A blind seminal receptacle tends to be a large, thick-walled structure, which is connected to the oviduct by a narrow duct: the sole remnant of the original Laurer's canal. This final development presumably means that the spermatozoa pass through Mehlis' gland in the opposite direction to that which normally occurs in the remainder of the hemiuroids. Spent spermatozoa and excess vitelline material are, therefore, voided via, or broken down and re-absorbed by, the uterus.

The evidence, which suggests that the presence of Laurer's canal opening to the exterior in conjunction with a uterine seminal receptacle is primitive, is that this is exactly the same arrangement which occurs in the majority of aspidogastreans (e.g. *Multicotyle*, *Lophotaspis*, *Cotylogasteroides*, *Macraspis*). The development of a seminal and vitelline disposal organ, however, is not limited to the Juel's organ of some hemiuroids. It appears that analogous structures may have developed in an aspidogastrean and certain turbellarians. Stafford (1896) described Laurer's canal of *Aspidogaster conchicola* Baer, 1826, as ending blindly in the form of a 'thick-walled bulb', and Voeltzkow (1888) refers to the same structure as a 'receptaculum vitelli' because it appeared to contain vitelline residues.* The absorption of excess sperm by the Turbellaria is discussed by de Beauchamp (1961, p. 31). He notes that, in addition to the genito-intestinal canal which occurs in some groups, there appear to be several different organs involved: these include the 'vesicle of Lang' of the polyclads (see Bock, 1927), the 'vesicula resorbiens' of the Kalyptorhynchia, and the copulatory bursa, which is found in many turbellarians. It is clear that, while there is a need to dispose of excess and spent seminal and vitelline material, there is in free-living helminths a strong selective pressure for the development of an organ of re-absorption, which thus aids the animal's economy. Owing to the ready availability of food, this pressure is probably much less in the parasitic forms, as demonstrated by the number of digeneans which still use Laurer's canal as a seminal and vitelline drain, but it would still appear to be advantageous to the economy of the parasite for it to develop a less wasteful system. If the actual biology of these digeneans is examined in detail, it is clear that many hemiuroids are stomach-parasites, and that they have developed mechanisms which protect them from the low pH and, in the case of marine teleosts, the high osmolarity of the environment (MacKenzie & Gibson, 1970; Gibson, 1971). The hemiurids which live in such conditions apparently withdraw their ecsoma and contract, with the result that they are protected by their thick tegument, and the derogenids from the stomach tend to migrate anteriorly towards the oesophagus during periods of low pH or high osmolarity. These parasites, therefore, contrary to intestinal forms, do not appear to be in a position to feed at all times. It would seem, consequently, that it is advantageous for these parasites to re-utilize some of its waste-material in order to help maintain egg-production during periods when feeding is limited.

The presence of a structure resembling a rudimentary Juel's organ in *Aspidogaster conchicola* does suggest that Juel's organ may also be a primitive feature; but this structure appears not to have been observed in other aspidogastreans. In addition, it appears that a similar structure may be present in digeneans unrelated to the hemiuroids, e.g. *Styphlodora bascaniensis* Goldberger, 1911 (see Goldberger, 1911*b*), and *Cyclocoelum sharadi* Bhalerao, 1935 (see Madhavi & Rao, 1974), and that this feature has not apparently been reported in other species of these genera which have been examined. It would seem, therefore, that a distal modification of Laurer's canal, which appears to be associated with the degradation of seminal and vitelline material, has been independently evolved on at least four different occasions. This would appear to vindicate Beklemishev's statement quoted above. Only in the hemiuroids, however, does this organ appear to have developed further, i.e. past the 'rudimentary' stage, and only in the hemiuroids is it common to entire groups. In other instances, it appears to have been developed independently by species, possibly recently, to meet their present ecological requirements. This is supported by the fact that none of the latter species are gut-parasites, and, therefore, such a development would probably be economically advantageous.

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* Voeltzkow claimed to have seen the canal open to the exterior in young animals, and that the 'receptacle' developed as the animal matured. Stafford, however, was of the opinion that Laurer's canal developed as an outgrowth from the oviduct.

Many digeneans have lost Laurer's canal, or have altered its function, i.e. in some groups it is used as a vagina. The latter occurrence we consider to be an advanced feature (Gibson & Bray, 1975), and species which use this method of copulation (one sided, as opposed to the possibility of reciprocal copulation where the genital atrium is used) normally have a thin-walled *canalicular seminal receptacle*, formed as a proximal dilation of Laurer's canal, and no uterine seminal receptacle, e.g. *Diphterostomum brusinae* (Stossich, 1889) and *Haploporus benedeni* (Stossich, 1887) – see Palombi (1931). We should emphasize that remarkably few digeneans have ever been seen in the act of copulation.

Assuming, from the above evidence, that the presence of Laurer's canal opening dorsally and a uterine seminal receptacle are, in the Hemiuroidea, primitive characters, it is not unreasonable to presume that Juel's organ has evolved in the manner described above. The derivation of the blind seminal receptacle of the opisthadenines and the majority of the lecithasterids from Juel's organ is not so obvious. If one discounts the possibility that it arose independently as a diverticulum of the oviduct, there appears to be only one other alternative. That is, its independent derivation from the rudimentary seminal receptacle. In the Lecithasteridae, *Trifoliovarium* has a large, functional canalicular seminal receptacle which has presumably evolved directly from a rudimentary seminal receptacle. The blind seminal receptacle of the related *Cladolecithotrema* has presumably evolved by the loss of Laurer's canal. Alternatively, in *Hysterolecitha* and presumably *Hysterolecithoides* Juel's organ is present. The blind seminal receptacle of the remainder of the lecithasterids could, therefore, have evolved from either a rudimentary seminal receptacle or Juel's organ. As the inner vesicle of Juel's organ appears to have been derived from the rudimentary seminal receptacle, this is essentially the same thing; but the thick, fibrous wall of the blind seminal receptacle is quite different to the relatively thin-walled type of seminal receptacle which usually occurs in digeneans. This suggests that the wall of the blind seminal receptacle may be derived from the outer capsule of Juel's organ. There is also evidence that the blind seminal receptacle of the opisthadenines has evolved from Juel's organ of the hemiurids and, as discussed below, that a similar blind seminal receptacle appears to have arisen independently from Juel's organ in the Didymozooidea.

Although the form of the seminal storage and disposal system tends to be relatively constant within a family or subfamily, there is a notable exception to this. In the Derogenidae a variety of conditions occur: (1) many halipegines, such as *Halipegus*, possess Laurer's canal, which opens dorsally, and a uterine seminal receptacle; (2) other forms, such as the Gonocercinae, are similar except that a small, but distinct, rudimentary seminal receptacle occurs; (3) in the remainder of the halipegines, such as *Genarchopsis* [but see p. 79] and *Arnola*, a fully developed Juel's organ is present; and (4) in the derogenines a continuous variation of conditions occur: (a) *Derogenes* possesses a large rudimentary seminal receptacle containing spermatozoa which is connected by Laurer's canal to a rudimentary Juel's organ; (b) in *Progonus* the rudimentary seminal receptacle is further enlarged to function as the only seminal store, the uterine seminal receptacle being lost, and the rudimentary Juel's organ is present at the junction of the seminal receptacle and Laurer's canal, which ends blindly; and (c) in *Leurodera* Laurer's canal and the rudimentary seminal receptacle appear to have been lost, leaving a blind seminal receptacle. The variation which occurs in this group can perhaps be explained by the fact that it is a large, successful group, possibly with primitive origins, arising at about the time when the first variations of the primitive seminal storage and disposal apparatus, such as the development of Juel's organ, were beginning to occur. It is possible that parallel evolution is responsible for some of the conditions which occur in this group and their apparent similarity to the arrangements in other hemiuroid groups.

(2) *Vitellarium*. There appears to be a very clear trend in the form of the vitellarium in the Hemiuroidea. Briefly, commencing with a follicular form, and passing through tubular and seven-lobed stages, the vitellarium is finally reduced to two, or occasionally one, oval masses. The trend begins with the follicular vitellarium which occurs in the Azygiidae (Fig. 7; arrangement A).

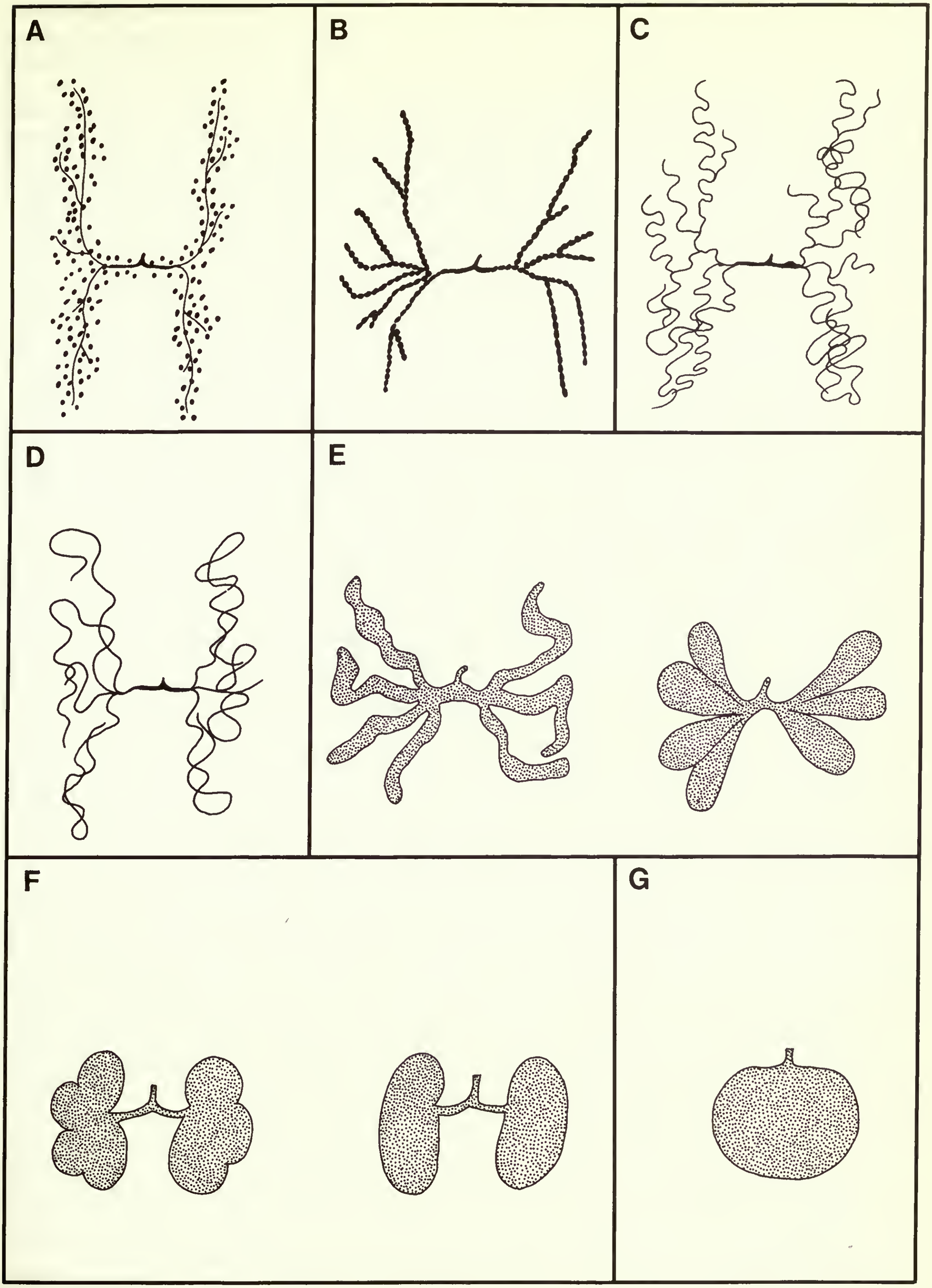

Fig. 7 Different arrangements of the vitellarium (see text).

These follicles become linked together along the collecting ducts, thus giving a chain-like appearance, as occurs in the syncoeliid *Otiotrema* and to some extent in the accacoeliid *Tetrochetus* (Fig. 7; arrangement B). The vitellarium then becomes distinctly tubular, consisting of many long, often convoluted, tubules, which may be branched (Fig. 7; arrangement C). The latter type of vitellarium occurs in the Accacoeliidae, Hirudinellidae and Isoparorchiidae. The next stage is that the number of tubules, which are usually unbranched, is reduced to seven: these usually being arranged with three on one side of the body and four on the other (Fig. 7; arrangement D); e.g. some sclerodistomids and some hemiurids, such as *Dinurus* and *Stomachicola*. The length of the seven tubules is then gradually reduced, so that they pass through digitiform (e.g. *Lecithocladium*, *Plerurus*, *Ectenurus*), tear-shaped (e.g. *Elytrophallus*, *Lecithaster*, *Hysterolecitha*) and oval (*Prolecitha*, *Dichadena*, *Lecithophyllum*, *Syncoelium*) stages (Fig. 7; arrangement E). The seven lobes, whether tubular, digitiform, tear-shaped or oval, may form a rosette arrangement, with three lobes on one side and four on the other, or may form two separate groups of three and four lobes which are connected by the collecting ducts. Presumably from the latter arrangement have developed forms, such as *Dinosoma* and *Arnola*, with two vitelline masses which are distinctly three- and four-lobed (Fig. 7; arrangement F). The lobation then tends to be almost or entirely lost (e.g. *Hemiurus*, *Brachyphallus*), resulting in forms, such as *Derogenes*, *Lethadena* and *Myosaccium*, with two totally unlobed, oval masses. In genera such as *Bunocotyle*, *Monolecithotrema*, *Monovitella* and *Chenia* the vitellarium is present as a single entire or slightly lobed mass (Fig. 7; arrangement G). This mass was probably, and almost certainly in the latter two cases, formed from the fusion of two oval masses; but there is a possibility that it could be the result of either the loss of one mass or the condensation of a rosette-arrangement.

It must be emphasized here that the above is only a general trend in the form of the vitellarium, as there is a certain amount of variation within each group, particularly within the hemiurids and the lecithasterids. For example, a relatively common feature of the lecithasterids is a doubling of the number of vitelline lobes. In addition, the number of vitelline tubules or lobes, commonly seven in many of the hemiuroids, is variable, six, eight or nine frequently being reported. The presence of nine (four and five) lobes is especially common on the two vitelline masses of the halipegine derogenids.

As the various links in the above pattern do appear to illustrate the trend relatively clearly, the only real problem is to find evidence which indicates that the follicular arrangement of the vitellarium is primitive. It appears, however, that a follicular vitellarium is found in the majority of monogenean and cestode groups, in all aspidogastreans and also in some rhabdocoel turbellarians, e.g. *Mesostoma*. This suggests very strongly that the follicular arrangement is primitive. It is likely that the duplication of the vitelline glands, resulting in the follicular arrangement, occurred as an early development to accommodate an increase in egg-production. This would have been especially necessary when the 'ancestral rhabdocoel' became an obligate parasite. This is emphasized by evidence from the digenean *Schistosoma mansoni* Sambon, 1907, which indicates that thirty to forty vitelline cells are present in each egg (Gönnert, 1955). The widespread spacial arrangement of this highly metabolically active organ-system in the 'primitive' forms is probably a mechanism to aid the absorbtion of nutrients from the surrounding parenchymatous tissue, rather like the roots of a tree. Even though food is often continually available to the 'primitive' hemiuroids, such as the azygiids and hirudinellids, they tend to be rather large for digeneans, and, therefore, still have certain problems with regard to the diffusion of nutrients. The more 'advanced' hemiuroids tend to be smaller in size, and, therefore, there is no longer such a need for a widespread follicular, dendritic or simple tubular vitelline system, as the problems associated with the diffusion of nutrients are reduced. In addition, there is more competition for space, as the uterus tends to take up a much greater proportion of the body. This latter factor, plus the economic advantage in reducing the distance involved in the transportation of vitelline material, adequately explains the reduction of the vitellarium to a small rosette or to one or two masses.

One apparent contradiction is the vitelline structure of the syncoeliine syncoeliids, which, as it consists of seven oval lobes, indicates that it is far more 'advanced' than the remainder of the anatomy. The premature reduction in the size of the vitellarium can be explained, however, by certain modifications in the process of egg-formation which appear to occur in this group. Our observations suggest that the eggs of *Copiatestes* are produced in a uterine oötype (see glossary), have a membranous 'shell' and contain only one, or a very small number, of vitelline cells. During the egg's passage down the uterus the vitelline cell(s) appear to replicate many times, the membranous 'shell' permitting the diffusion of nutrients into the egg as a source of material and energy for this process. Not until a full complement of vitelline cells is present, at about the middle of the uterus, does the egg-shell become thicker, tanned and hardened. The demand on the vitellarium for vitelline cells appears, therefore, to be greatly reduced, possibly by a factor of twenty to thirty times. Some aspects of egg-shell formation have been described by Gibson (1976) for *Copiatestes filiferus* (Leuckart, in Sars, 1885) and by Coil & Kuntz (1963) for the related *Syncoelium spathulatum* Coil & Kuntz, 1963.

3. *Terminal genitalia.* The terminal genitalia of the Hemiuroidea show a great number of modifications; but do in fact, with a small number of exceptions, illustrate one basic trend. There are, however, a number of variations in the general pattern, and it is likely that some features of this trend have been evolved independently by parallel evolution. In order to understand both the nature of the trend and the variation, we must first examine the function of these structures. The function of the male terminal genital apparatus is that of ejecting spermatozoa and enabling it to enter the female system, either of another worm or of the same individual. The function of the female terminal genitalia is that of ejecting eggs into the environment, and, we suggest in the case of the Hemiuroidea, receiving spermatozoa from the male terminal genitalia of either another worm or of the same individual. As indicated above, it is clear from our studies of Laurer's canal (Gibson & Bray, 1975) that in the Hemiuroidea, when this duct is present, it functions as a seminal and vitelline drain, not as a vagina (*Trifoliovarium* may be an exception). Evidence from the work of Nollen (1968), who used ^{3}H-thymidine-labelled spermatozoa in *Philophthalmus megalurus* (Cort, 1914) suggests that cross-insemination occurs in the majority of cases whenever possible; but that, when only single worms are present in a host, self-insemination occurs regularly. Nollen also noted that labelled spermatozoa disappeared from the uterine seminal receptacle within fourteen to sixteen days of copulation, which indicates that repeated insemination is required. It would appear, therefore, that self-insemination is a mechanism which has evolved to enable lone specimens in a host to produce fertile eggs. It seems very likely that in some genera self-insemination has become increasingly important, to the extent that the male copulatory apparatus has atrophied. In some cases, such as *Bathycotyle*, *Gonocerca*, *Aerobiotrema*, *Syncoelium* (sensu stricto) and *Tetrochetus*, where the copulatory apparatus has completely disappeared or has been reduced to a vestige, they must, it appears, rely solely upon self-insemination. It is likely that the latter phenomenon has occurred independently in several different groups both within and outside the Hemiuroidea. To illustrate this point, the terminal genitalia and the seminal storage and disposal system of the opecoeline opecoelids are almost identical to those which occur in *Gonocerca*. Too much systematic importance, therefore, should not be placed upon the absence or reduction of the copulatory apparatus.

The main trend in the structure of the terminal genitalia of the Hemiuroidea appears to be as follows. It commences as a simple sinus-organ, produced as a protrusion of the base of the genital atrium, and containing both of the simple, tubular male and female ducts. These ducts come together and unite near the summit of this organ, forming a short hermaphroditic duct which opens via a terminal pore. The close proximity of the male and female ducts which opens into a common genital atrium aids both reciprocal cross-insemination and self-insemination, and, similarly, the development of an hermaphroditic duct further facilitates self-insemination. This latter arrangement (Fig. 8; arrangement A) occurs in the azygiids, where the sinus-organ is a highly contractile, permanent structure, but is usually found in a relatively contracted state. The sinus-organ of the azygiids, which presumably acts as a copulatory organ and possibly aids the extrusion of eggs through the genital pore, is formed from the proximal region of the wall of the genital atrium, and it uses its own intrinsic musculature for extension and contraction. The genital atrium presumably serves as a vagina during copulation, and it is likely that the muscular

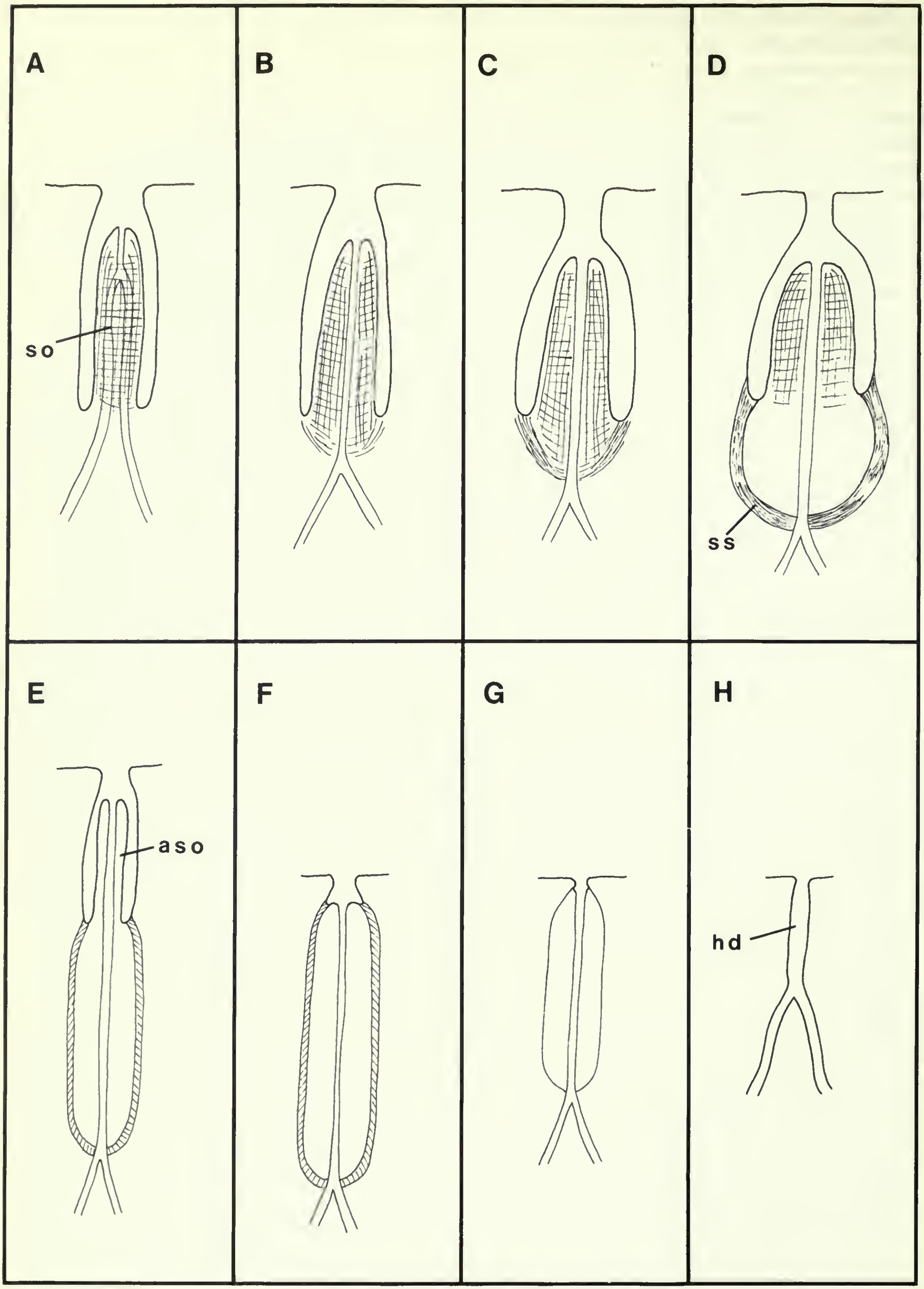
A
B
C
D
so
ss
E
F
G
H
aso
hd

Fig. 8 Different arrangements of the terminal genitalia (see text). [aso, amuscular sinus-organ; hd, hermaphroditic duct; so, muscular sinus-organ; ss, sinus-sac.]

action of its wall forces the spermatozoa, deposited during copulation, back into the hermaphroditic duct through the aperture of the contracted sinus-organ.

Following on from the type A arrangement, the sinus-organ becomes a relatively larger structure in its contracted state, and some of its intrinsic musculature begins to concentrate into a thin, diffuse sac-like structure surrounding its base (Fig. 8; arrangement B). At the same time, the hermaphroditic duct tends to lengthen, usually reaching at least to the base of the sinus-organ. This arrangement can be seen gradually developing in *Prosorchis*, *Copiatestes*, *Isoparorchis*, *Sclerodistomum*, *Accacoelium* and *Prosogonotrema*, resulting in a type C arrangement (Fig. 8) where the diffuse, muscular thickening at the base of the sinus-organ, which is referred to as the sinus-sac, becomes more apparent in the latter four examples, and, in addition, the intrinsic musculature of the sinus-organ itself tends to become slightly reduced. We consider that the sinus-sac aids the extrusion of the sinus-organ by exerting hydrostatic pressure upon its contents (Gibson & Bray, 1974). Many of the derogenids tend to have an arrangement very similar to that of *Prosogonotrema*, except that the cone-shaped sinus-organ tends to be small. In the dinurine hemiurids the sinus-sac is better developed (Fig. 8; arrangement D), becoming an enlarged oval or tubular structure with a thick, muscular wall, and the sinus-organ is usually cone-shaped, often with a slight reduction in its intrinsic musculature. The sinus-organ may be large, as in *Paradinurus*, or small, as in *Dinurus*, and it should be mentioned that in a small number of dinurines, such as *Stomachicola*, the sinus-organ is absent or reduced to a rudiment: in the latter cases the sinus-sac is also reduced in size. It is noticeable that at about the stage of the type D arrangement, the seminal vesicle, which until now has normally been tubular, tends to become more saccular and often develops sphincters and thus becomes partitioned. These appear to be modifications caused by the fact that, during ejaculation, the spermatozoa now have to be forced into the hermaphroditic duct against the hydrostatic pressure produced when the sinus-sac aids the eversion of the sinus-organ. The next stage (Fig. 8; arrangement E) is that the intrinsic musculature of the sinus-organ is then lost, resulting in the fact that it must be entirely everted by hydrostatic pressure. This arrangement can be seen in the Elytrophallinae and in the Glomericirrinae, especially in the former, where the sinus-organ appears to be almost totally amuscular, the sinus-sac is well developed and the seminal vesicle is surrounded by an extremely thick muscular wall. The latter structure is presumably necessary because of an increased hydrostatic pressure necessary to evert the sinus-organ. In the next stage (Fig. 8; arrangement F) the genital atrium is reduced in size and a permanent sinus-organ is lost. The latter is replaced by a short, temporary sinus-organ, rarely seen in fixed specimens, which is formed by evagination of the hermaphroditic duct under hydrostatic pressure. As the hydrostatic pressure is less than that required in the type E arrangement, because of the much smaller sinus-organ and genital atrium, pressure is usually exerted on the seminal vesicle by sphincter muscles or by a thin, muscular layer in its wall, rather than by a thick, muscular wall. This arrangement occurs in the Hemiurinae, Lecithochiriinae, *Stomachicola* and a small number of related dinurines, the Opisthadeninae, the Lecithasterinae and the Quadrifoliovariinae. Finally, in the Hysterolecithinae, Trifoliovariinae, Lethadeninae, Plerurinae, Macradenininae, Dictysarcinae, Prolecithinae and Gonocercinae, the sinus-sac is gradually atrophied (Fig. 8; arrangement G) until in genera such as *Aerobiotrema* and *Gonocerca*, it is lost completely (Fig. 8; arrangement H). Presumably, as mentioned above, in the latter groups the ability to cross-inseminate becomes reduced and is finally lost altogether. It is worth noting that there is a slight deviation within the Hemiuridae, in that the Glomericirrinae, with the type E arrangement, and the Lecithochiriinae, with the type F arrangement, have developed an ejaculatory [prostatic] vesicle. This appears to be a modification of the ejaculatory duct, the function of which is not known for certain. It may, however, form a temporary storage organ as part of a mechanism for ejecting larger quantities of spermatozoa during each ejaculation. If this is true, then the glandular cells, which often line it, may function, with regard to the stored sperm, in the same way that the pars prostatica does to normal quantities of sperm passing through this duct during ejaculation.

One group, the Hirudinellidae, stand out as being totally distinct from the remainder of the hemiuroids in that they possess a 'cirrus-sac'. This structure almost certainly developed independently of the sinus-sac; but it does appear to be analogous. The reason why such a structure has developed in this group is probably because its ancestors lost, or did not develop, an hermaphroditic duct, with the result that the copulatory organ ('cirrus') did not contain the female duct. In this group, therefore, both the male and the female ducts have developed their own finger-like projections from the wall of the genital atrium. It seems certain that the 'cirrus-sac' of the hirudinellids is not homologous with the cirrus-sac which is found in many other groups of digeneans. At first sight, it is somewhat difficult to see how the hirudinellid arrangement could have evolved from the type A arrangement; but other morphological features of the hirudinellids suggest a relatively close affinity with some of the other 'primitive' hemiuroids. For this reason, it seems unlikely that the hirudinellids split away very early in hemiuroid evolution before the development of an hermaphroditic duct. It is possible, however, to envisage the gradual separation of the male and female ducts of the type A arrangement, where the hermaphroditic duct is short, much in the same way as appears to have occurred in some species of *Halipegus*, where the two ducts open separately at the end of the sinus-organ. It is very unlikely that the Hirudinellidae resemble the ancestral form of the hemiuroids, as it is difficult to imagine how an hermaphroditic duct could have been derived from the hirudinellid arrangement.

We can assume that the presence of apparatus well adapted to enable cross-insemination to occur is the primitive condition in the hemiuroids, as cross-insemination occurs in all other groups of helminths. Even in the primitive hemiuroids, however, it is almost certain that self-insemination does occur, and Dawes (1946) notes that self-insemination of lone specimens of the aspidogastrean *Aspidogaster conchicola* has been observed. It seems likely that the type A arrangement in our trend is primitive. It is a fact that the majority of hemiuroids differ from the majority of helminths in that the copulatory organ is not the usual cirrus, which is often enclosed by a cirrus-sac. Nevertheless, all of the structures termed 'cirrus' are not homologous, as the copulatory organs of many groups of animals have a phallic appearance. In addition, it is unlikely that all of the structures termed 'cirrus-sac' are homologous, as similar 'sacs' surround the base of, and are associated with the protrusion of, many eversible organs, e.g. the proboscis sac of the Acanthocephala. If we examine the aspidogastreans, the majority of species do possess a cirrus-sac, but several do not. There appears to be no evidence in the latter group for the presence of an hermaphroditic duct. As it seems difficult to envisage the development of an hermaphroditic duct, similar to that occurring in the hemiuroids, from a form with a cirrus-sac, it is possible that the rhabdocoel-like ancestors of the digeneans possessed a temporary penis-papilla ('cirrus'), lacking a penis-bulb ('cirrus-sac'), which was formed from the wall of the genital atrium. Commencing with such a structure, it is possible to envisage the development of all of the variations of the terminal genitalia which occur in the Digenea and Aspidogastrea.

A suggested evolutionary scheme within the Hemiuroidea

Published works on evolution within the Digenea are few. Aspects of this subject have been discussed by workers such as Odening (1974), and detailed comments on particular groups have been given by others, such as Bayssade-Dufour & Maillard (1974); but only a few workers, such as Poche (1926) and Cable (1974), appear to have indicated detailed evolutionary relationships within the Digenea as a whole. The majority of evidence in the more recent work has come from larval morphology and details of the life-history. As discussed in our introduction, we believe that much of the evidence based upon such information is questionable. Admittedly data from the intra-molluscan stages are likely to be of some value, but only at the higher taxonomic levels, and, as indicated on p. 38, there are some anomalies. If, as Rohde (1972) suggests, the cercariae were 'invented' by the digenean ancestors as a mechanism to aid the transmission from the molluscan host to the vertebrate host, evidence based upon cercarial morphology, especially as this larval stage is more susceptible to environmental changes than the others, is somewhat dubious. Although the majority of phylogenetic hypotheses on the evolution of and within the Digenea have been based upon larval characteristics, there is evidence that workers are beginning to reappraise the value of adult morphology. Powell & Sogandares-Bernal (1970), for instance, stated: 'While on the subject of larval trematodes, the systematic value of comparative anatomical studies of the terminal genitalia and sensory structures of adult worms should be emphasized.

Homologies and analogies of terminal genitalia (for example in the Hemiuroidea) should prove useful in determining phylogenetic relationships.'

Using evidence outlined in the trends illustrated above, we have attempted to build a hypothetical picture of the evolution of the Hemiuroidea. Our proposed relationships are expressed in Fig. 9. We believe that the most primitive groups are the azygiids and the ptychogonimids, and that the most closely related of these to the ancestors of the remainder of the hemiuroids appear to be the leuceruthrine azygiids. These groups exhibit a combination of primitive characters, such as a follicular vitellarium, a sinus-organ without an accompanying sinus-sac and with Laurer's canal acting as a seminal and vitelline drain. The Leuceruthrinae, which appears to exist as a single species, possesses the same gonadal arrangement as that which occurs in the vast majority of the remainder of the hemiuroids. Another interesting feature which may indicate primitiveness in this group is that in known azygiid life-cycles the cercariae are eaten directly by the definitive host. This suggests the possibility that the azygiids evolved before the acquisition of the second intermediate host which occurs in most digenean life-cycles. Other primitive groups are the Hirudinellidae, Bathycotylidae, Isoparorchiidae, Syncoeliidae, Accacoeliidae and Sclerodistomoididae, and it seems likely that they, especially the latter four, have arisen from a common ancestor. Nevertheless, there are features of the syncoeliids, such as the presence of seven vitelline lobes in the syncoeliines, which suggest that they are more advanced than indicated by the position which we have allocated to them in our 'evolutionary picture'; but, as discussed above (p. 126), these anomalies can be explained. In the latter groups a sinus-sac develops (a 'cirrus-sac' in the case of the hirudinellids) and the vitellarium becomes tubular. In our opinion the remainder of the hemiuroids have evolved from an ancestor resembling the present-day sclerodistomids, although most probably lacking Manter's organ and with more posteriorly situated gonads. From this ancestral form, which presumably possessed a vitellarium consisting of seven tubules, a well-developed sinus-organ and sinus-sac, and Laurer's canal (which although opening dorsally was on the point of evolving a rudimentary Juel's organ), four main lines appear to have evolved. These are: (1) the modern members of the Sclerodistomidae; (2) the Derogenidae; (3) the Lecithasteridae, Dictysarcidae and the Didymozooidea (see p. 133); and (4) the Hemiuridae and Bunocotylidae. The development of Juel's organ, in the rudimentary and or the fully developed form, has occurred in all of these groups. As forms with Laurer's canal opening dorsally also occur in three of the groups, it seems more likely that Juel's organ has arisen independently by parallel evolution than by the concurrent evolution of forms with and without this organ in all of these three groups.

The sclerodistomids are the only one of these groups which either have not developed a complete Juel's organ or in which no members of the group possessing such an organ survive, although rudimentary forms occur in *Prosogonotrema* and *Prosorchis*. It would appear that despite the position of the gonads, the prosogonotrematine and prosorchiine genera are perhaps more closely related to the other three groups outlined above than the sclerodistomines.

The Derogenidae are a very successful group with a complex mixture of primitive and advanced features, especially with regard to the nature of the seminal storage and disposal apparatus in the female reproductive system. Nevertheless, the majority of members tend to be relatively similar in gross morphology, although it seems likely that the three subfamilies of this group separated quite early in the evolution of the group. They probably owe their success to the fact that they tend to fill niches where competition is somewhat reduced, i.e. the stomach of oceanic fishes, in the case of the Gonocercinae and the Derogeninae, and both the stomach of brackish water and freshwater fishes and the mouth and eustachian tubes of amphibians, in the case of the Halipeginae.

The Lecithasteridae appear to have evolved via forms similar to *Trifoliovarium*, but still retaining a uterine seminal receptacle and a rudimentary seminal receptacle. From this form developed the modern members of the Trifoliovariinae and, after the independent formation of Juel's organ, the Hysterolecithinae. The remainder of the lecithasterids could have evolved from forms similar to *Trifoliovarium* by the loss of Laurer's canal, much in the same way as *Cladolecithotrema* has probably developed; but it seems more likely that they have evolved from hysterolecithine ancestors. This is suggested by the great morphological similarity between the

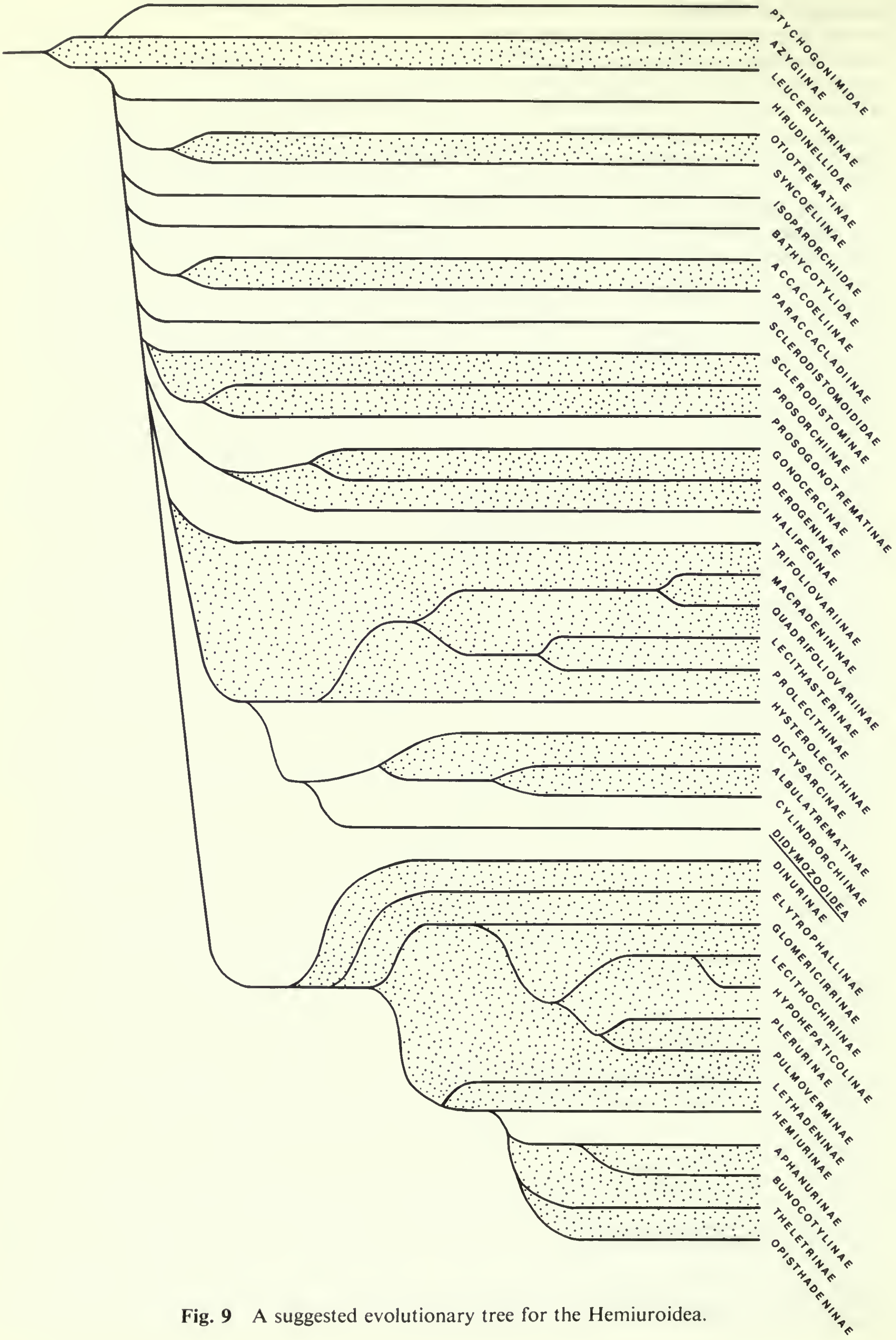
PTYCHOGONIMIDAE
AZYGIINAE
LEUCERUTHRINAE
HIRUDINELLIDAE
OTIOTREMATINAE
SYNCOELIINAE
ISOPARORCHIIDAE
BATHYCOTYLIDAE
ACCACOELIINAE
PARACCACLADIINAE
SCLERODISTOMOIDIDAE
SCLERODISTOMINAE
PROSORCHIINAE
PROSOGONOTREMATINAE
GONOCERCINAE
DEROGENINAE
HALIPEGINAE
TRIFOLIOVARIINAE
MACRADENININAE
QUADRIFOLIOVARIINAE
LECITHASTERINAE
PROLECITHINAE
HYSTEROLECITHINAE
DICTYSARCINAE
ALBULATREMATINAE
CYLINDRORCHIINAE
DIDYMOZOOIDEA
DINURINAE
ELYTROPHALLINAE
GLOMERICIRRINAE
LECITHOCHIRIINAE
HYPOHEPATICOLINAE
PLERURINAE
PULMOVERMINAE
LETHADENINAE
HEMIURINAE
APHANURINAE
BUNOCOTYLINAE
THELETRINAE
OPISTHADENINAE

Fig. 9 A suggested evolutionary tree for the Hemiuroidea.

Hysterolecithinae and some of the other lecithasterids and because the thick-walled nature of the blind seminal receptacle in the rest of the lecithasterids suggests that it might have evolved from Juel's organ by hypertrophy of the 'inner vesicle'. It is also apparent, because of the presence of Juel's organ and other morphological similarities, that not only the Dictysarcidae, but also the Didymozooidea (see below), may have evolved from hysterolecithine ancestors.

In the largest group, the Hemiuridae, an ecsoma in association with a plicated tegument appears to have developed (see p. 41), although the former is occasionally reduced and the latter is often completely lost. These adaptations appear to be associated with the hostile habitat of the majority of hemiurids, the stomach of marine teleosts which is a region of variable pH and osmolarity. The most primitive group appears to be the Dinurinae, some of which have features in common with some of the modern sclerodistomids, although all appear to possess a fully developed Juel's organ. The dinurines probably gave rise to the elytrophallines by the development of an amuscular sinus-organ and associated changes in the seminal vesicle. The elytrophallines could then have given rise to: (1) the Glomericirrinae, by the development of an ejaculatory (prostatic) vesicle, which in turn gave rise to forms, such as the Lecithochiriinae, by the loss of a permanent sinus-organ; and (2) the Hemiurinae and the Lethadeninae, by the loss of a permanent sinus-organ. The Bunocotylidae appear to have evolved from ancestral hemiurines by the loss of the ecsoma. It is worth noting that some members of the Aphanurinae still retain a plicated tegument. In the members of the Bunocotylinae, which are extremely small, Juel's organ appears to have been lost, there apparently being no obvious mechanism for disposing of excess seminal and vitelline material. It is possible that these compact and apparently advanced worms utilize not only space, but also spermatozoa and vitelline material, more efficiently, thus reducing the value such a specialized organ. In the opisthadenines Juel's organ appears to have developed into a blind seminal receptacle, much in the same way as we suggest it developed in the majority of the lecithasterids.

Throughout the evolution of this group it is clear that there is a general decrease in body-size, ranging from the giant azygiids and hirudinellids to the minute bunocotylids. Associated with this decrease in size is a more efficient utilization of body-space, such as the development of a compact vitellarium, and a more efficient utilization of excess reproductive products. In addition, although less certain, there appears to be an increase in the proportion of the body occupied by the uterus, and an increase in the dependency upon self-fertilization, thus reducing the need for large and complex terminal genitalia.

Some comments on the relationship of the Didymozooidea and the Paramphistomoidea to the Hemiuroidea

The Didymozooidea are a group which several early workers, such as Odhner (1907) and Poche (1926), considered to be evolved from hemiuroid stock. This early work was based upon adult morphology. Baer & Joyeux (1961), however, basing their hypothesis on the work of Ishii (1935) which indicated that adults of this group developed directly from eggs, recognized the Didymozoidea as a new subclass, distinct from the Digenea, within the class Trematoda. Recently Cable (1955, 1974), using evidence from larval stages, has reiterated Odhner's initial hypothesis that this group is derived from hemiuroid stock. Skrjabin (1955) and Yamaguti (1971) present the didymozooids as a distinct suborder and superfamily, respectively, to the hemiuroids, but do not comment on any relationship between the two.

If those didymozooid genera with a simpler and more conventional morphology, such as *Nematobothrium* van Beneden, 1858,* are examined, several similarities with the hemiuroids are apparent. The testes are normally pre-ovarian and the ovary normally occurs anterior to the vitellarium. The male and female terminal ducts fuse, often forming a short hermaphroditic duct, and open via a common genital pore, and in some instances a small terminal papilla not unlike a sinus-organ is present. In addition, the shape and arrangement of the gonads in juvenile specimens of *Didymocystis acanthocybii* Yamaguti, 1938 (as figured by Yamaguti, 1970), are very similar to those of the dictysarcid hemiuroid *Elongoparorchis*. More convincing, however, are the facts that a uterine seminal receptacle is present in *Nematobothrium robustum* Yamaguti, 1970, and that Odhner (1907) has described what appears to be a well-developed Juel's organ in the closely related *N. scombri* (Taschenburg, 1879) (Fig. 10A). Although the latter structure in *Nematobothrium* spp. has usually been referred to as a seminal receptacle, Yamaguti (1970), when describing *Neonematobothrioides poonui*, noted that it contained germ-cells and vitelline material, in addition to spermatozoa. An apparent Juel's organ was also seen by Dollfus (1935) in *Nematobothrium pelamydis* (Taschenburg, 1879). Juel's organ of the didymozooids appears to differ slightly from that in the hemiurids, for example, in that the 'inner vesicle' is not completely enclosed proximally by the outer region of the organ, suggesting that it is perhaps slightly more primitive (see p. 121). The presence of Juel's organ and a uterine seminal receptacle, however, does not appear to be the usual condition in the more highly developed didymozooids. In the majority of these cases the uterine seminal receptacle has apparently been lost and Juel's organ appears to have become transformed into a blind seminal receptacle, which is connected to the oviduct by a short duct, much in the same way as blind seminal receptacles have probably been formed in the majority of lecithasterids and the opisthadenine bunocotylids. In sections of an unidentified didymozooine [close to *Didymocystis* Ariola, 1902] from *Katsuwonus pelamys* off Papua New Guinea, the outer half of the blind seminal receptacle has a thick wall, possibly being the vestige of the outer region of Juel's organ, and the inner half (that closest to the duct) of this seminal receptacle has a thin wall, possibly being formed from the part of the 'inner vesicle' not enclosed by the outer region of Juel's organ (Fig. 10B).

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* The conception of the genus used here is that of Yamaguti (1971).

These observations on the gross morphology and on the nature of the seminal storage and disposal apparatus in the proximal female reproductive system of certain didymozooids suggest to us that this group did evolve from hemiuroid stock close to the origins of the Dictysarcidae probably from an ancestral form of hysterolecithine lecithasterid (see Fig. 9).

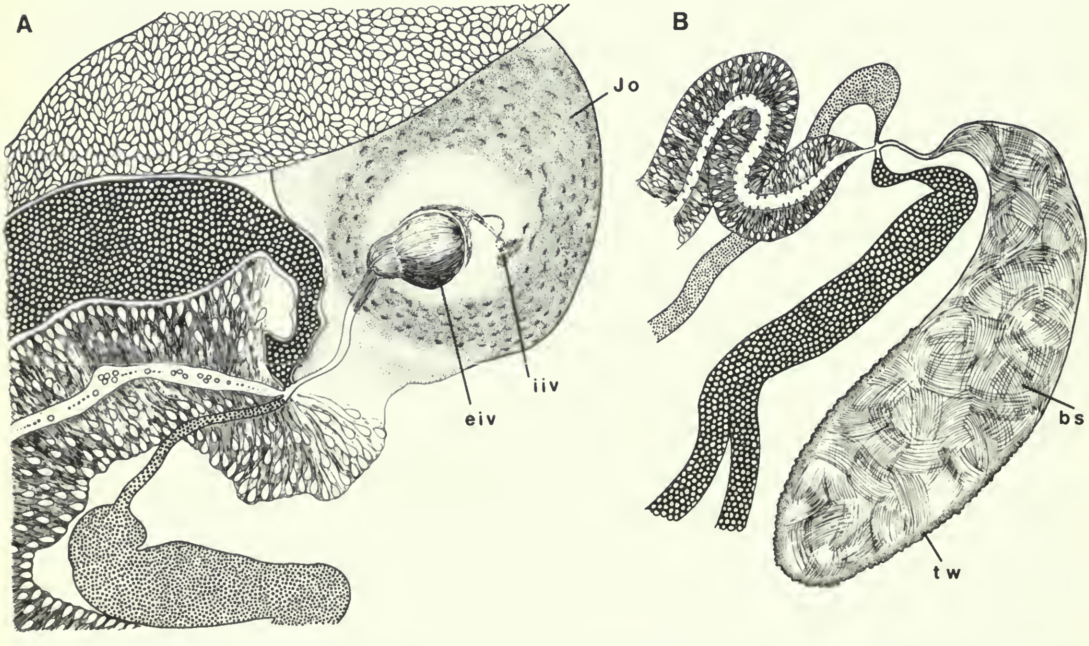

Fig. 10 Parts of the seminal storage and disposal apparatus in the female reproduction system of two didymozooids: A. *Nematobothrium scombri* (modified after Odhner, 1907); B. Unidentified didymozooine. [bsr, blind seminal receptacle; eiv, external 'inner vesicle'; iiv, internal 'inner vesicle'; Jo, Juel's organ; tw, thick-walled region of blind seminal receptacle.]

It is also worth noting that there are certain morphological features which suggest that there may be affinities between the paramphistomoids and some of the more primitive hemiuroids. These include a follicular vitellarium, the absence of a prepharynx, paired testes which are usually pre-ovarian, the presence of Laurer's canal in association with a uterine seminal receptacle and similar terminal genital apparatus. The paramphistomoids differ fundamentally in adult morphology only in the fact that the excretory pore is dorsal rather than being terminal. Although the hindbody is almost absent in this group, there is also a tendency for its reduction in certain hemiuroids, especially in the Sclerodistomidae. The paramphistomoids are generally considered to be stomach parasites of terrestrial vertebrates: several genera have, however, been recorded from teleosts. One particular group, the Brumptiidae Stunkard, 1925, appears to be morphologically very similar to the hemiuroids in that its members possess a well-developed sinus-sac and an hermaphroditic duct, and, in the lateral fields, there is a distinct hindbody present in the form of lobes, being somewhat similar to, but smaller than, those which occur in the syncoeliid *Otiotrema*.

Although workers such as Dawes (1936) have considered the paramphistomoids to be very primitive, Cable (1974) places this group well up one of the branches of his evolutionary tree. He also places it on quite a distinct branch to the hemiuroids, although Poche (1926) had placed them much closer together. Evidence from adult morphology suggests that the paramphistomoids might have been derived from hemiuroid stock close to the point where the syncoeliids and hirudinellids evolved. Nevertheless, there does appear to be fundamental differences in the morphology of the larval stages and the life-history which tend to preclude any serious consideration of this relationship until the significance of these differences is fully understood.

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Introduction

The purpose of this paper is three-fold; to describe certain anatomical features of the piscivorous cyprinid *Macrochirichthys macrochirus*, to account for their structure in terms of function, and on the basis of those features considered to be derived ones, to postulate the taxon's relationships. The identification and assessment of these characters has led to a reappraisal of the Cultrinae, the subfamily to which *Macrochirichthys* is presently assigned, and to the delimitation of a monophyletic assemblage which includes *Macrochirichthys* but excludes many of the genera currently placed in the Cultrinae.

In an earlier paper describing in part the musculature and skeletal elements of *Macrochirichthys* (Howes, 1976), I pointed out a convergence (see p. 184) between this species and the characoid *Rhaphiodon*. The present studies (on *Macrochirichthys*) enable further comparisons to be made of skeletal and myological architecture in these two cypriniform genera.

Nomenclatural note

The relatively unfamiliar generic name *Securicula* Günther 1868 is introduced early in this paper. This name is used in place of *Pseudoxygaster* Bănărescu 1967 for which reasons are stated on p. 191.

List of study material

Much of the material listed in a previous study (Howes, 1978) was re-examined and only additional specimens used for the present study are given here.

Bull. Br. Mus. nat. Hist (Zool.) **36** (3) : 147–200 Issued 27 September 1979

Species	BMNH register number	Locality	Standard length (mm)
Aspidoparia jaya	1889.2.1 : 937–46	Hardawar	66, 67
Aspidoparia morar	1938.2.22 : 32–38	Darna, R., Bombay Prov.	62, 64, 65
Aspidoparia morar	1872.4.17 : 81	Bengal	92, 93
Barbichthys laevis	1866.5.2 : 113	Unknown	213
Barilius barila	1889.9.26 : 131–140	Deoli	83
Chela cachius	1889.2.1 : 1340–7	Orissa	24–37
Chela laubuca	1889.2.1 : 1356–9	Madras	61
Chela laubuca	1889.2.1 : 1349–54	Orissa	Alizarin
Chelaethiops elongatus	1975.6.20 : 308–340	Laulaba R.	63, 54
Danio aequipinnatus	1889.2.1 : 1295–7	Sadya	71
Danio dangila	1889.2.1 : 1292	Darjeeling	60
Danio devario	1973.2.26 : 1–6	Bengal	45–74
Danio malabaricus	1889.2.1 : 1252–7	Wynad	63–67
Danio malabaricus	1889.2.1 : 1298	Deccan	78
Danio spinosus	1889.2.1 : 1250	Burma	58
Engraulicypris minutus	1955.12.20 : 1021–27	Tanganyika L.	55–67
Engraulicypris sardella	1932.11.15 : 181–220	Malawi L.	62–90
Esomus danrica	1863.12.8 : 108–114	Madras	82
Hemiculter bleekeri	1964.5.4 : 1–2	Shanghai	90
Hemiculterella polylepis	1921.7.26 : 21–28	Yunnan L.	114
Ischikauia steenackeri	1900.9.29 : 38–39	Tokyo	145, 122
Macrochirichthys macrochirus	1866.5.2 : 46	Unknown	198
Macrochirichthys macrochirus	1922.5.19 : 1	Tembeling R., Malay Peninsula	402
Macrochirichthys macrochirus	1898.4.2 : 243	Menam R.	212
Macrochirichthys macrochirus	1898.11.8 : 121	Menam R.	Skeleton
Macrochirichthys macrochirus	1978.1.10 : 1–4	Kapuas R.	160–182
Macrochirichthys macrochirus	Unregistered	Borneo	32
Macrochirichthys macrochirus	Unregistered	Borneo	Alizarin 30
Megalobrama bramula	1936.10.19 : 21	Hankow	112
Nematabramis alestes	1933.3.11 : 58–65	Culion, Philipines	70
Opsariichthys bidens	1902.5.30 : 45–54	S. Hupeh, China	40–89
Oxygaster anomalura	1889.11.12 : 82	Sumatra	136
Oxygaster anomalura	1881.3.21 : 3	Sarawak	178–190
Oxygaster hypophthalmus	1895.2.28 : 66	Sarawak	98
Oxygaster maculicauda	1939.6.27 : 1–2	Sumatra	29–32
Oxygaster oxygastroides	1897.10.8 : 138–140	Bangpakong R.	90–114
Oxygaster oxygastroides	Unregistered	Unknown	Alizarin; 38
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Parachela breitensteini	Vienna Museum P3000	Borneo	Holotype, 97
Paralubuca typus	1883.7.4 : 84–87	Mekong	95, 101
Pelecus cultratus	1966.2.22 : 1–2	S. Rumania	170–173
Pelecus cultratus	1876.4.12 : 1	Platten See	223–237
Plagiognathops microlepis	1896.6.8 : 23	Kiu Kiang	248
Pseudolaubuca sinensis	1889.6.24 : 61	Kiu Kiang	172 Skeleton
Rasbora argyrotaenia	1974.10.10 : 1801–05	Bali	78
Rasbora einthovenii	1970.9.3 : 31–50	Singapore	32
Rasbora elegans	1970.9.3 : 555–584	Singapore	57, 85
Rasbora rasbora	1894.1.19 : 69–75	Sarawak	57–66
Rasborinus lineatus	1937.9.17 : 5–9	Annam	75
Rutilus rutilus	Unregistered	Thames	Alizarins

Species	BMNH register number	Locality	Standard length (mm)
Salmostoma bacaila	1889.9.26 : 145–154	Deoli, India	Alizarin *c.* 75
Salmostoma bacaila	1889.2.1 : 1443–5	Central Prov.	106, 113, 52
Salmostoma boopis	1889.2.1 : 1411–2	Canara	77
Salmostoma clupeoides	1968.2.22 : 52–56	Darna R.	192–82
Salmostoma phulo phulo	1889.2.1 : 1467	Godavery R.	84
Salmostoma phulo phulo	1889.2.1 : 1406	Assam	54
Salmostoma phulo orissaensis Holotype	1889.2.1 : 1403	Orissa	54
Salmostoma phulo orissaensis Paratype	1889.2.1 : 1404	Orissa	45
Salmostoma sardinella	1891.11.30 : 374–83	Sittany R.	96–95
Salmostoma untrahi	1889.2.1 : 1746	Mahannddi R.	94
Salmostoma untrahi	1889.2.1 : 1747–51	Orissa	65–90
Securicula gora	1889.2.1 : 1373	Assam	126
Securicula gora	1934.10.17 : 54	Allahabad	138
Securicula gora	1870.6.14 : 27	Unknown	170
Securicula gora	Unregistered	Unknown	Alizarin 93
Toxabramis swinhonis (Syntypes)	1873.7.30 : 97	Shanghai	77–80
Xenocypris davidi	1969.4.15 : 85	Szechwan	224
Xenocypris tumirostris	1969.4.15 : 69	Szechwan	227
Xenocypris yunnanensis	1921.7.26 : 24–28	Yunnan L.	90

All the specimens were dissected and radiographed.

Abbreviations used in the text figures

AA	Anguloarticular
AS	Axial scale
BO	Basioccipital
CCF	Cleithrum-coracoid fenestra
CF	Carotid foramen
CL	Cleithrum
CIM	Cranial intermuscular bones (numbered)
COR	Coracoid
D	Dentary
Depx	Dorsal section of *epaxialis* muscle
ECT	Ectopterygoid
ENT	Entopterygoid
EPO	Epioccipital
ES	Extrascapular
Ets	Tendinous midline septum of *epaxialis*
EXO	Exoccipital
FC	Frontal sensory canal
FR	Frontal
F IV	Foramen for trochlear nerve
F V	Foramen for *trigemino-facialis* trunk
Hlms	Horizontal lateral myoseptum
HMP	Hyomandibular process
Hms	Medial segment of *hypaxialis* muscle
HY	Hyomandibula
Hypx	*Hypaxialis* muscle
IF	Infraorbitals (numbered)
KE	Kinethmoid
Lap 1, 2	*Levator arcus palatini* muscle, divisions 1 and 2
LE	Lateral ethmoid
Lepx	Lateral *epaxialis* muscle
LIM	Lateral intermuscular bones
LKE	Kinethmoid–mesethmoid ligament
LP2	Lateral process of 2nd vertebra
Ls	*Lateralis superficialis* muscle
ME	Mesethmoid
MQF	Metapterygoid-quadrate fenestra
Ms	Myosepta
MX	Maxilla
NC	Neural complex
NP2 & 3	Neural process of 2nd and 3rd vertebrae
NS	Neural spine (numbered)
Obi	*Obliquus inferioris* muscle
Obs	*Obliquus superioris* muscle
OP	Operculum
OS	Os suspensorium

PA	Parietal
PAL	Palatine
PAS	Parasphenoid
PC	Postcleithrum
PCP	Posterior coracoid process
PE	Preethmoid
PMX	Premaxilla
PRO	Prootic
PTS	Pterosphenoid
PTT	Posttemporal
Q	Quadrate
QF	Quadrate foramen
RA	Retroarticular
SC	Supracleithrum
Sca	*Supracarinalis anterior* muscle
SE	Supraethmoid
SN	Supraneural (numbered)
SO	Supraoccipital
SOR	Supraorbital
SPO	Sphenotic
SY	Symplectic
TR	Tripus
Tsca	Tendon of *supracarinalis anterior* muscle
V	Vertebra (numbered)
Vebx	Ventral section of *epaxialis* muscle
VC1	Cartilage block between ventral process of 1st vertebra and limb of 2nd vertebra
VO	Vomer
X	Axis of vertebral column

Anatomical notes on *Macrochirichthys macrochirus*

After each descriptive section there follows a comparison with other cultrine and in some cases, non-cultrine genera.

The most outstanding features of *Macrochirichthys* are the almost straight to convex dorsal head profile, the oblique angle of the mouth and the greatly extended pectoral fins (Fig. 1). The body is elongate, tapering caudally and is markedly compressed with a prominent ventral keel; the scales are small, *c.* 120 in the lateral line, the lateral line is curved gently downwards and runs almost midlaterally; the dorsal and anal fins are placed far back; the length of the pectoral fin is almost twice that of the head and its tip extends to a point nearly half-way along the standard length; the pelvic fins are situated midway between the base of the pectorals and the origin of the caudal fin. The fish is intensely silver along the flanks, brassy dorsally and with a large black blotch at the base of the caudal fin. Juvenile specimens possess dark saddle-like markings between the head and the dorsal fin. Smith (1945) reports specimens of more than half a metre in length.

There appears to be only a single species referrable to this genus (see Smith 1945 : 77–78 and p. 187). It is recorded from Thailand, Java, Sumatra, Borneo, Cambodia, Laos and south China (Weber & De Beaufort, 1916; Smith, 1945; Wu, 1964; Taki, 1974).

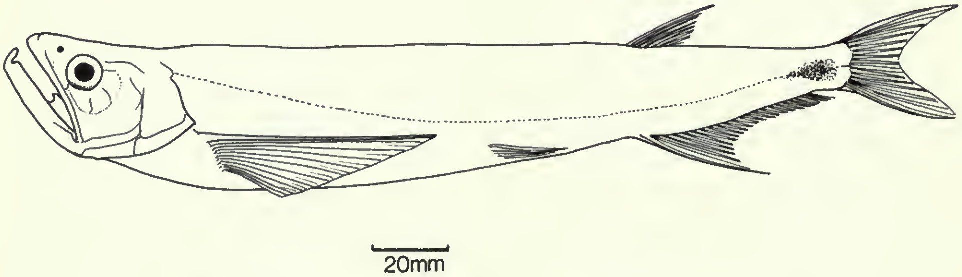

Fig. 1. Outline drawing of *Macrochirichthys macrochirus.*

Cranium

The horizontal dorsal outline of the head does not indicate the top of the cranium but marks the edge of the thick wedge of epaxial muscle mass that extends forward as far as the anterior border of the frontals. The cranium itself is aligned at an angle of 20° to the vertebral column (see p. 171). The skull is narrow and is, to the best of my knowledge, the most compressed in any cyprinid.

The *frontals* curve medially so as to form an elongate basin into which the epaxial muscle mass inserts (Fig. 2A). Laterally, each frontal is folded over to form a creased edge. Anteriorly the

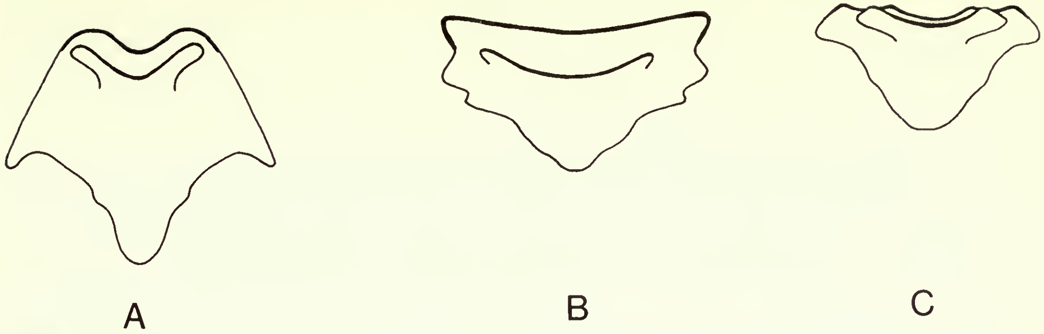

Fig. 2 Cross-sections of the crania of A. *Macrochirichthys macrochirus*. B. *Securicula gora*. C. *Parachela oxygastroides*. Two sections are shown, through the sphenotic region (entire outline) and through the anterior part of the ethmoid region (inset outline). The extent of the frontals are indicated by the thickened line.

frontals overlie the supraethmoid and cover that bone almost to its anterior margin (see below). In adults the frontal sensory canals converge to share a common opening at the midline (Fig. 3). In juveniles (30 mm SL) the frontals have not developed the concavity seen in the adult but are flat and the epaxial musculature extends only as a thin band along the midline to the anterior tip of the bones. Furthermore, at this stage of development the frontals have not extended forward to cover the supraethmoid and the sensory canals do not meet (cf. Figs 3 & 4).

For the *ethmoid region* the use of the terms *supraethmoid* and *mesethmoid* follows that of Weitzman (1967), Patterson (1975) and Dornesco & Soresco (1971). The *supraethmoid* is the

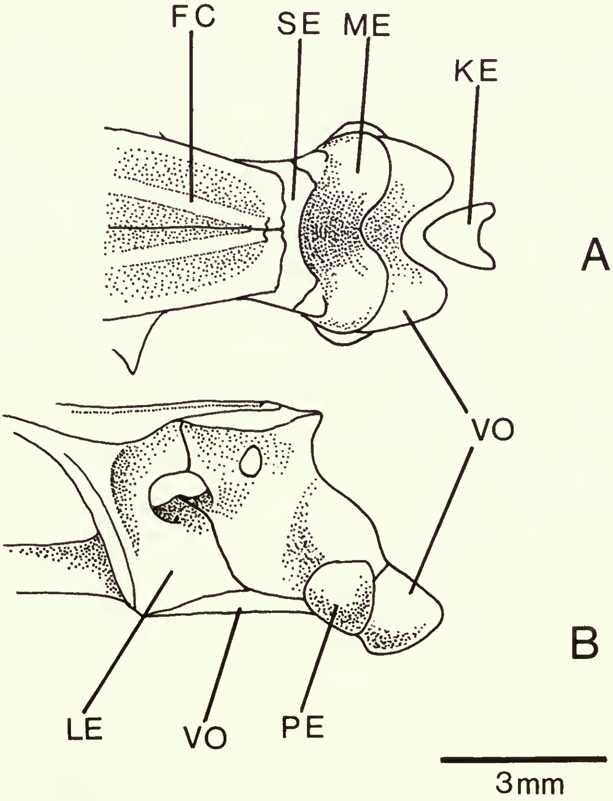

Fig. 3 *Macrochirichys macrochirus* ethmo-vomerine region in A. Dorsal view. B. Lateral view.

dermal bone overyling the ethmoid cartilage and in small specimens can be clearly distinguished as a separate element (see below); in some larger specimens although its anterior and lateral sutures can be defined, the supraethmoid is more often than not fused with the underlying, and ossified, ethmoid cartilage (*mesethmoid*). The term *ethmoid block* is used here to denote the entire unit comprising the supraethmoid, mesethmoid and preethmoids.

In adult *Macrochirichthys* the supraethmoid is short, barely projecting from below the frontals. Its anterior border is concave; on either side protrudes the forwardly curved mesethmoid; thus the entire region presents a concave anterior face which slopes downward to join the underlying vomer (Fig. 3).

The *vomer* extends anteriorly well beyond the mesethmoid and is deeply notched (Fig. 3). Posteriorly it extends to below the suture of the mesethmoid with the lateral ethmoids. Laterally, the lower part of the mesethmoid and the upper part of the vomer are recessed to receive the wedge-shaped *preethmoids.*

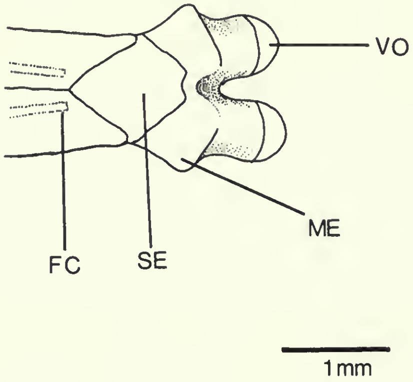

Fig. 4 *Macrochirichthys macrochirus.* Dorsal view of the anterior part of the cranium of a juvenile (30 mm SL).

In specimens of 30 mm SL the shape of the ethmoid block differs from that in the adult (Fig 4). The supraethmoid is well-defined and is covered by the frontals only along its V-shaped posterior margin; the anterior concavity of the ethmoid block is far more pronounced, with a greater anterior and lateral extension than in adult specimens. The vomer is exposed below the anterior extensions of the ethmoid block and is not visible in the midline when viewed from above.

The *kinethmoid* (Figs 3 & 5A) fits into the anterior ethmoid notch, its contacting face curved in both the vertical and transverse planes. Dorsally the kinethmoid is expanded into two lateral wings which curve forward to enclose the tips of the premaxillary ascending processes. Two ligaments connect the kinethmoid to each face of the mesethmoid.

The depression of the cranium has resulted in the *orbitosphenoids* being shallow and in close contact with the parasphenoid. Contact is *via* a septum derived mainly from the orbitosphenoids and only partly from the parasphenoid.

The postero-ventral border of each *pterosphenoid* contacts the respective ascending process of the parasphenoid; the posterior border is bounded by the prootic and the sphenotic (Fig. 6).

The *prootic* is a long, depressed bone bearing a long lateral commissure across the trigemino-facialis chamber, the anterior foramen of which is situated on the border of the prootic (Fig. 6).

The *sphenotic* is narrow and is curved downwards as an almost perpendicular surface. The sphenotic process, which in most cyprinids extends laterally as a thick spine, is here developed as a wide, ventrally directed arm (Fig. 6).

Each *parietal* covers an extensive area of the cranium, overlying the medial part of the pterotic so that it extends to the lateral edge of the cranium (Fig. 6).

The *supraoccipital* is a large bone with a shallow medial ridge extending posteriorly as a lamellar process. On either side of the ridge the supraoccipital is formed into a hummock.

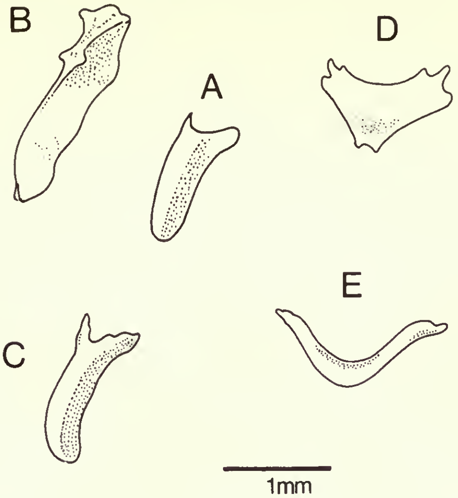

Fig. 5 Kinethmoids of A. *Macrochirichthys macrochirus*, B. *Securicula gora*, C. *Parachela oxygastroides*, D. *Chela laubuca*, E. *Danio malabaricus*. Lateral oblique views.

The *subtemporal fossae* have considerable depth because of the high vaulting of the cranium in the parietal–supraoccipital region. Posttemporal fossae are absent.

Comments and comparisons
The overlapping of the supraethmoid by the frontals is a character shared with *Securicula*, *Salmostoma*, *Chela*, *Aspidoparia*, *Rasborinus* and some species of *Rasbora* and *Danio*. In all other cyprinids I have examined the supraethmoid meets the leading edge of the frontals in a close suture. An exception is in some species presently assigned to the African genus *Engraulicypris*; work is in progress on this group and for the time being it can be stated that the presence of this feature in '*Engraulicypris*' is considered a parallelism.

The supraethmoid of *Securicula* is larger than that of *Macrochirichthys*, its anterior border is convex and, furthermore, the arms of the ethmoid block do not diverge to the same extent (Fig. 7). A similar type of morphology to that of *Securicula* is found in *Salmostoma*, while in *Oxygaster*

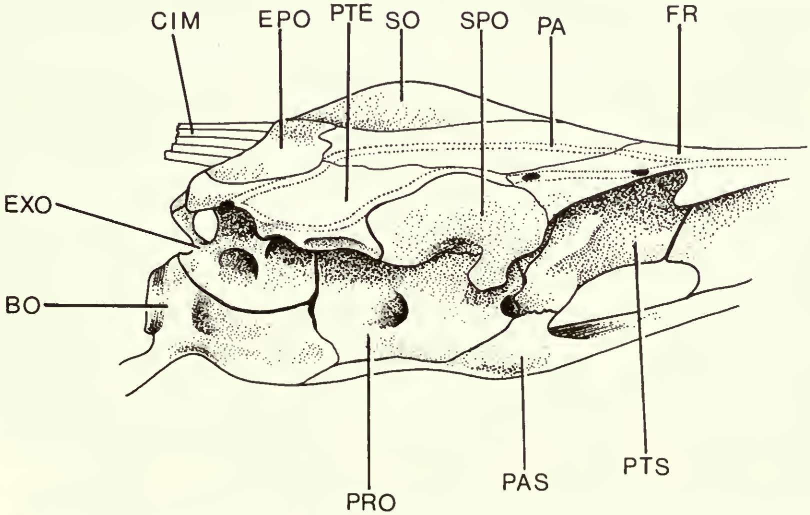

Fig. 6 *Macrochirichthys macrochirus*, lateral view of the posterior neurocranium.

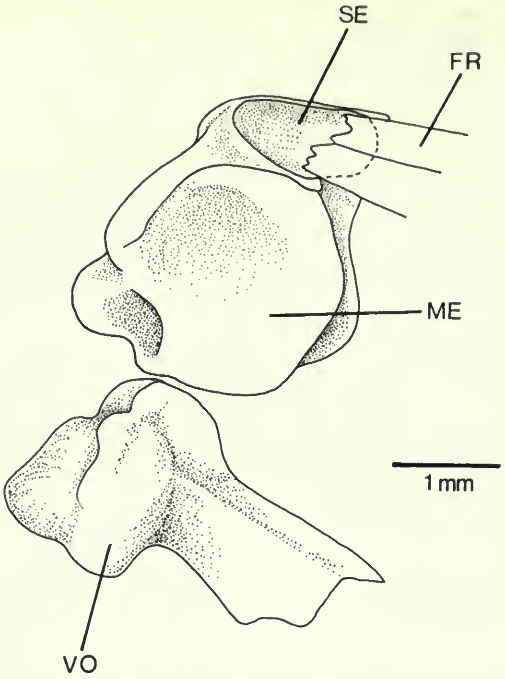

Fig. 7 *Securicula gora*, ethmo-vomerine region in dorso-posterior oblique view. Vomer separated from mesethmoid.

the narrow supraethmoid with its concave border and the diverging arms of the underlying mesethmoid more closely resemble the condition in *Macrochirichthys.*

In *Chela* the supraethmoid is a narrow, axe-shaped bone covering only the medial area of the underlying mesethmoid (Fig. 8). The mesethmoid projects far beyond the lateral edges of the supraethmoid (a condition encountered in juvenile *Macrochirichthys*, see above, p. 152). Antero-ventrally the ethmoid block extends forward as a thin shelf; the vomer is considerably reduced in thickness and lies as a thin plate below the medial and lateral ethmoids with only its posterior margin contacting the parasphenoid.

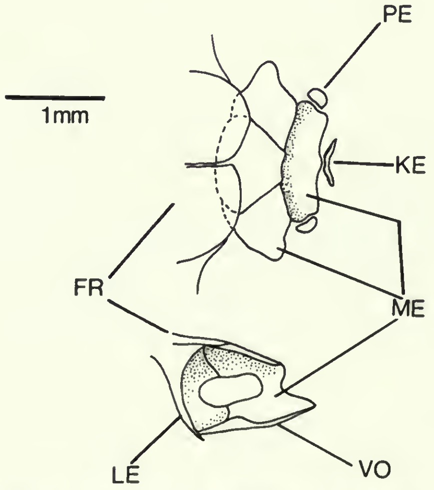

Fig. 8 *Chela laubuca*, ethmo-vomerine region in A. Dorsal, B. Lateral views.

The morphology of the ethmo-vomerine region of some *Rasbora* species resembles that in *Chela*, particularly in the development of the thin ethmoid shelf and the kinethmoid (see below).

In other cultrines (e.g. *Culter* and *Erythroculter*) the supraethmoid is thick and posteriorly is sutured to the frontals (Fig. 9A). The mesethmoid is long and overlies the vomer for most of its length. The preethmoids are large and extend to beyond the border of the vomer. A similar condition exists in *Pseudolaubuca* but here the entire ethmoid block is deepened (Fig. 9B). A similarly deep ethmoid region is found in *Pelecus* (Fig. 9D). The morphology of these cultrine genera differs from that in other cyprinids (exemplified by *Opsariichthys*, Fig. 9C) where the vomer is exceedingly thick, the supraethmoid is reduced in length (but wide and laterally overlapping the mesethmoid) and the preethmoids extensive.

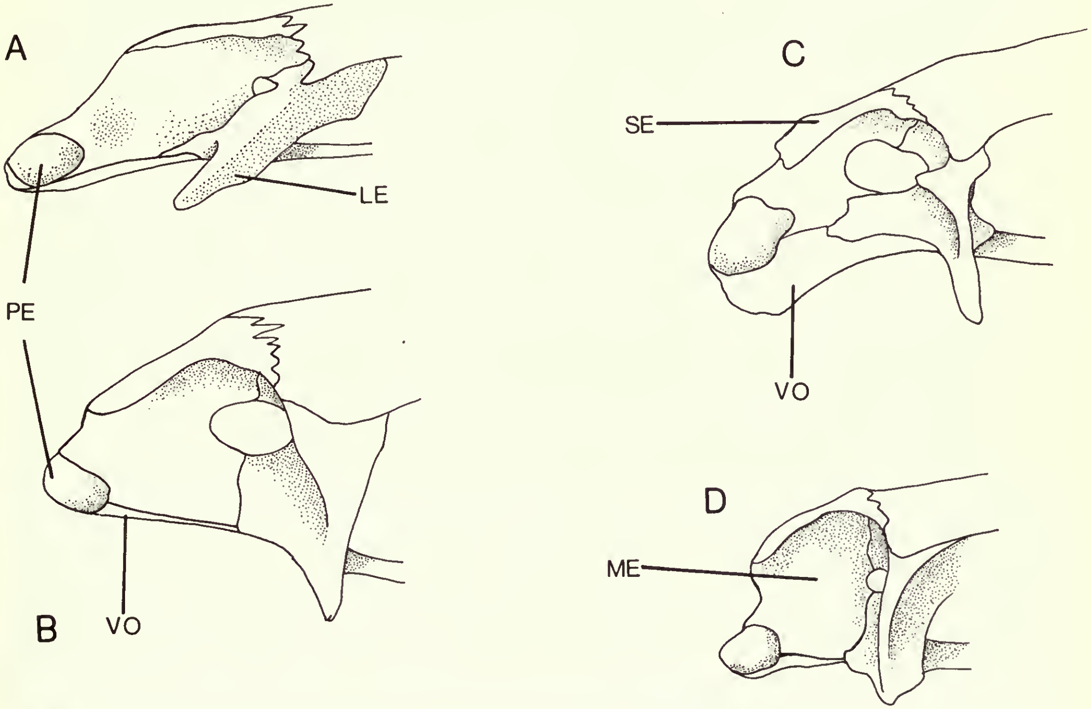

Fig. 9 Ethmo-vomerine regions of A. *Culter alburnus*, *Pseudolaubuca sinensis*, C. *Opsariichthys uncirostris*, D. *Pelecus cultratus*. Lateral views.

The dorsal expansion of the kinethmoid found in *Macrochirichthys* is also present in *Oxygaster* (Fig. 5C); in some species the lateral wings of the kinethmoid project anteriorly to articulate with the premaxillaries, as in *Macrochirichthys* (Fig. 5A). In *Securicula* there is no great dorsal expansion of the kinethmoid; instead small extensions are present on either side and serve for the insertion of the ligaments connecting the bone to the mesethmoid (Fig. 5B). However, the anterior tip of the kinethmoid is convex instead of concave (as it is in *Macrochirichthys* and *Oxygaster*) and it is connected with the premaxillaries *via* ligaments and not direct bony projections. In *Chela* and *Rasbora* (some species) the kinethmoid is lamellar and broadly triangular, and its dorsal border is concave (Fig. 5D). In these taxa the bone is inclined backward and lies against the protruding shelf when the jaws are opened. Although in *Danio* (some species) the triangular outline of the bone is preserved, the kinethmoid is modified into a bow-shaped structure (Fig. 5E).

The medial depression of the frontals is a character shared with three other genera, *Securicula*, *Oxygaster* and *Pelecus*. However, in *Securicula* the frontals are wider and the medial depression shallower; also, the lateral edges of the frontals are curved upwards and the inner branch of the frontal sensory canal is curved mesially to meet its counterpart some-way back from the anterior edge of the bone (Fig. 10). Of the five species assigned to the genus *Oxygaster* (see Bănărescu, 1969), all apart from *O. anomalura* share with *Macrochirichthys* the same narrow and deeply depressed frontals; likewise the frontal sensory canals converge anteriorly to share a common opening. In *Oxygaster anomalura* the frontals are flat without the medial groove and the sensory canals are confined to the lateral edges of the bones. In *Pelecus*, although the frontals bear a depression similar to that of *Macrochirichthys* they do not overlap the supraethmoid anteriorly; also, the sensory canals are restricted to the lateral margins of the bones and are much ramified and, furthermore, the frontals partly cover the sphenotic so as to form a roof for the dilatator fossa. The dilatator fossa in *Macrochirichthys* is not roofed and in *Securicula* and *Oxygaster* it is overlapped by the pterotic.

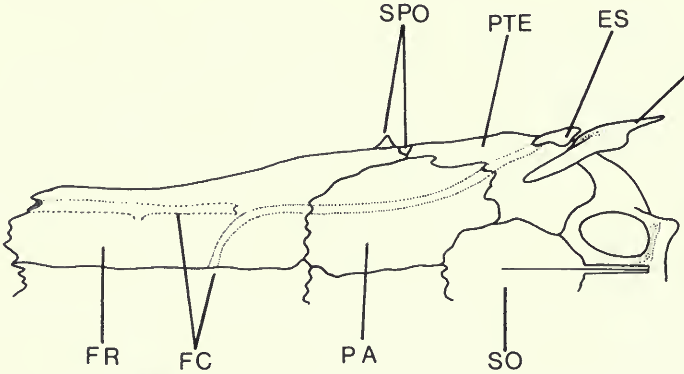

Fig. 10 *Securicula gora*, dorsal view of cranium.

In *Securicula* the sphenotic bears a small, laterally directed process (Fig. 10). A similar process is also present in *Oxygaster* but is directed ventro-posteriorly. The pterotic in *Securicula* contributes more to the dorsal surface of the cranium than it does in *Macrochirichthys* and *Oxygaster*, and the posterior region of the skull is not so highly vaulted (Fig. 10).

In *Chela* and *Salmostoma* the parasphenoid and the orbitosphenoids are linked by a deep orbitosphenoid septum. In *Macrochirichthys*, *Securicula* and *Oxygaster* these bones are closely united. Mention of this feature was made by Howes (1978) and it has been noted that in other ostariophysans such close contact between the orbitosphenoids and parasphenoid is associated with a large gape (Howes, 1976; Menezes, 1976). There is an obvious functional advantage in such an arrangement; the area of the palatoquadrate arch is increased by moving the parasphenoid dorsally, while there is a concomitant increase in the volume of the buccal cavity. The close association of the parasphenoid with the cranial roof may serve to distribute the stresses imposed upon the cranium through the striking-type feeding action of these fishes. Although functional demands have undoubtedly influenced the development of this type of bone association, the degree of separation between the bones may well reflect phyletic affinities. Certainly in all species of *Salmostoma* there is a deep orbitosphenoid septum regardless of gape size, which shows interspecific variation.

In *Macrochirichthys* there is a lateral connection between the pterosphenoid and the ascending wing of the parasphenoid (p. 152, & Figs 6 & 11). This type of connection is encountered rarely in the cyprinids (see Howes, 1978). It occurs in some species of *Barilius* and *Luciosoma* but in the group of genera presently under discussion it occurs only in *Securicula*. In this taxon the connection between the two bones is extensive (reminiscent of the condition in some *Barilius*). A feature *Securicula* shares with *Salmostoma* is that the anterior trigemino-facialis foramen is situated within the face of the prootic and the lateral commissure is narrow. There is no connection between the parasphenoid and pterosphenoid in *Salmostoma*, *Oxygaster* or *Chela*, the pterosphenoid contacting only the prootic posteriorly (Fig. 11). Current studies on the bariliines and other cyprinids indicate that the lateral connection of the pterosphenoid and parasphenoid is a derived feature. It is usually achieved through a backward lengthening of the pterosphenoid and only a slight forward extension of the prootic. This forward movement of the prootic involves the wall anterior to the trigemino-facialis foramen and thus the foramen becomes placed within the prootic face (the condition encountered in *Securicula*). *Macrochirichthys* is unusual in that there has been no anterior lengthening of the prootic but a marked posterior extension. This has resulted in a long lateral commissure, but the anterior foramen of the trigemino-facialis chamber has remained on the border of the bone. It is also noted that there has been only a slight posterior extension of the pterosphenoid.

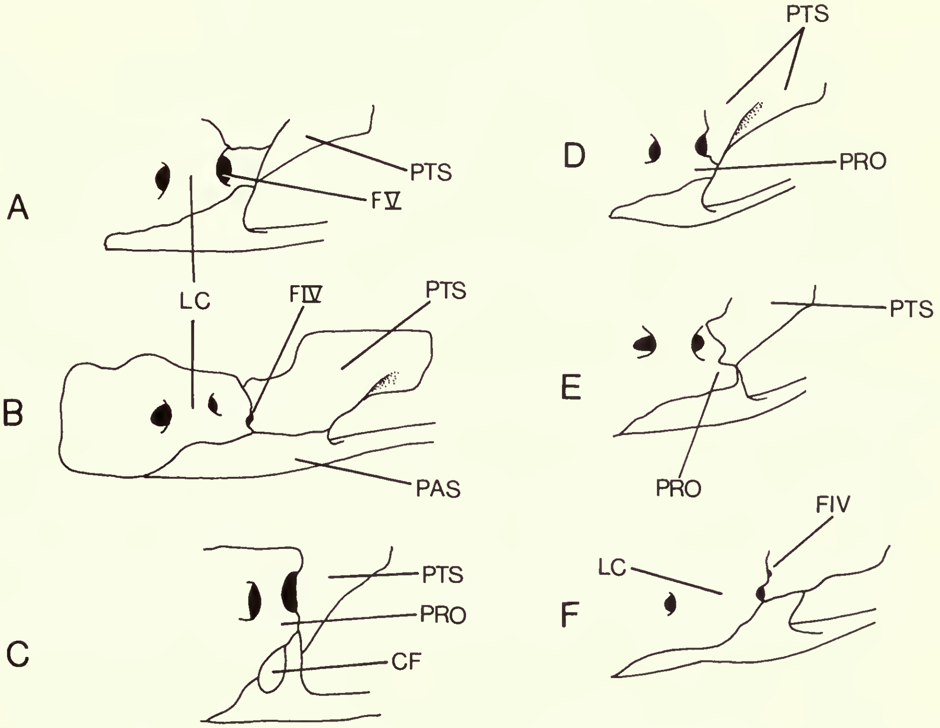

Fig. 11 Outline figures of prootic-pterosphenoid-parasphenoid junction in A. *Salmostoma bacaila*, B. *Securicula gora*, C. *Chela laubuca*, D. *Oxygaster anomalura*, E. *Parachela oxygastroides*, F. *Macrochirichthys macrochirus*.

In summary; the medially depressed cranium is a feature *Macrochirichthys* shares with *Securicula*, all but one species of *Oxygaster* and *Pelecus*. *Pelecus*, however, does not share with the others the overlap of the supraethmoid by the frontals. *Macrochirichthys* shares with all but one species of *Oxygaster* the convergence of the frontal sensory canals and with *Securicula* a lateral connection between the pterosphenoid and parasphenoid.

Circumorbitals (Figs 12 & 13)
The *supraorbital* of *Macrochirichthys* is reduced in the adult to a barely detectable splinter that has no contact with the 5th infraorbital. The *infraorbitals* are well-developed but the 4th does not cover the entire cheek and the 5th is reduced to a thin ossification around the sensory canal tube (Fig. 12A).

Comments and comparisons
A reduced supraorbital is present in *Securicula* (Fig. 12B), *Oxygaster* (Fig. 13), *Salmostoma* (Fig. 12C) and *Aspidoparia*, but in *Chela* and *Rasbora* it is wide (Fig. 12D). In *Culter*, *Erythroculter*

and most other cultrine genera the supraorbital is moderately developed. In *Pelecus* as in *Macrochirichthys*, the supraorbital is small, but unlike *Macrochirichthys*, the bone in *Pelecus* is expanded anteriorly and is in contact with the lateral ethmoid.

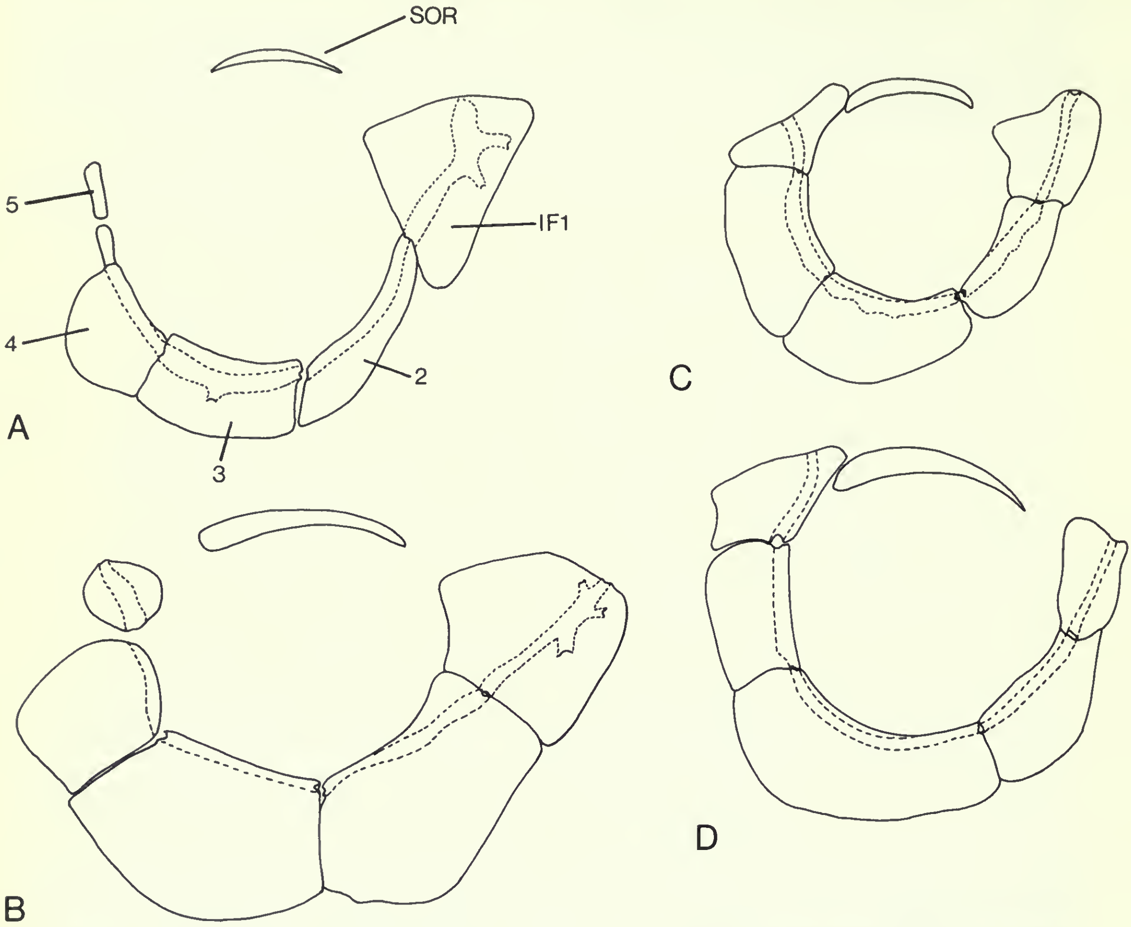

Fig. 12 Circumorbital series of A. *Macrochirichthys macrochirus*, B. *Securicula gora*, C. *Salmostoma bacaila*, D. *Chela laubuca*.

The infraorbitals of various cyprinids have been discussed at some length in an earlier paper (Howes, 1978) where it was noted that the 4th and 5th infraorbitals in many genera are reduced and that there is no contact between the 5th infraorbital and the supraorbital. In *Securicula* all the infraorbitals are well-developed, the 4th almost covering the cheek and the 5th also expanded (Fig. 12B). A similar degree of development is found in *Salmostoma*, *Aspidoparia*, *Chela* and *Rasbora* (Figs 12C & D). In *Oxygaster* the ossification of the 4th and 5th bones is reduced to almost the canal and the 5th contacts the supraorbital (Fig. 13). The canal running through the first infraorbital (lachrymal) is usually branched in most cyprinids, but in all the genera noted above (including *Macrochirichthys*) it is a straight unbranched tube.

Intermuscular bones and the body musculature (Figs 14–18)
The anterior intermuscular bones of *Macrochirichthys* are strongly developed. Five bones articulate with the posterior edge of the epioccipital, just medial to the pterotic (Fig. 14). All are almost equally developed needle-like elements whose distal surface bears a slight lamellar ridge.

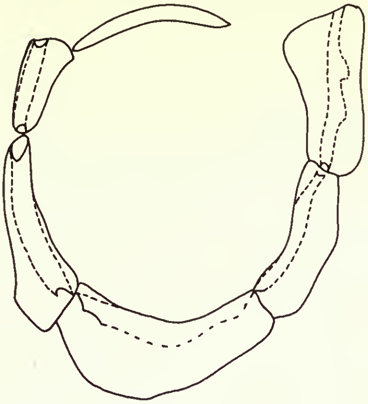

Fig. 13 Circumorbital series of *Parachela oxygastroides*.

The points of the bones extend to between the eleventh and fourteenth vertebrae. In a large specimen (212 mm SL) the bones are closely united anteriorly, one above the other, so as to form a laminated beam (Figs 14 & 15). Below this beam and running parallel to it, are another four or five intermuscular bones (LIM, Figs 15–18) but these have no connection with the cranium.

The *epaxialis* muscle can be regarded as being in two parts; an upper section (Depx, Figs 15–18) which reaches to the anterior part of the cranium, and a lower section (Vepx, Figs 16–18) lying medial to the intermuscular bone beam. In fact the two sections are merged and it is only the stratified nature of the lower part that enables such a division to be made (see below).

In the dorsal section of the *epaxialis* the fibres are long and are directed forward at an angle of 5° to the horizontal plane, and transversely at 3–5° to the medial plane. There are no distinct myomeres, their boundaries are indicated laterally by cord-like myosepta (Ms, Fig. 15) angled at 5° to the horizontal. Medially the 'myosepta' become tendinous bands which permeate the *epaxialis*. Anteriorly, a tendinous septum extends from the second neural plate and the neural complex (Ets, Fig. 16) to insert along the low supraoccipital crest.

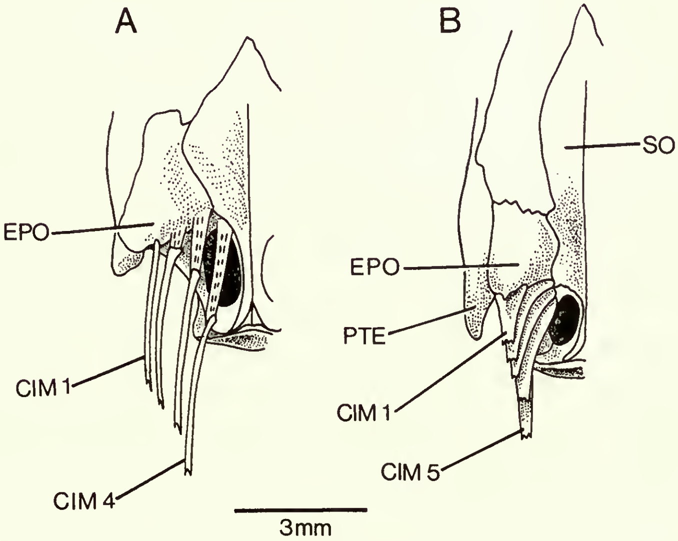

Fig. 14 Cranial intermuscular bones of A. *Securicula gora*, B. *Macrochirichthys macrochirus* seen in dorsal view.

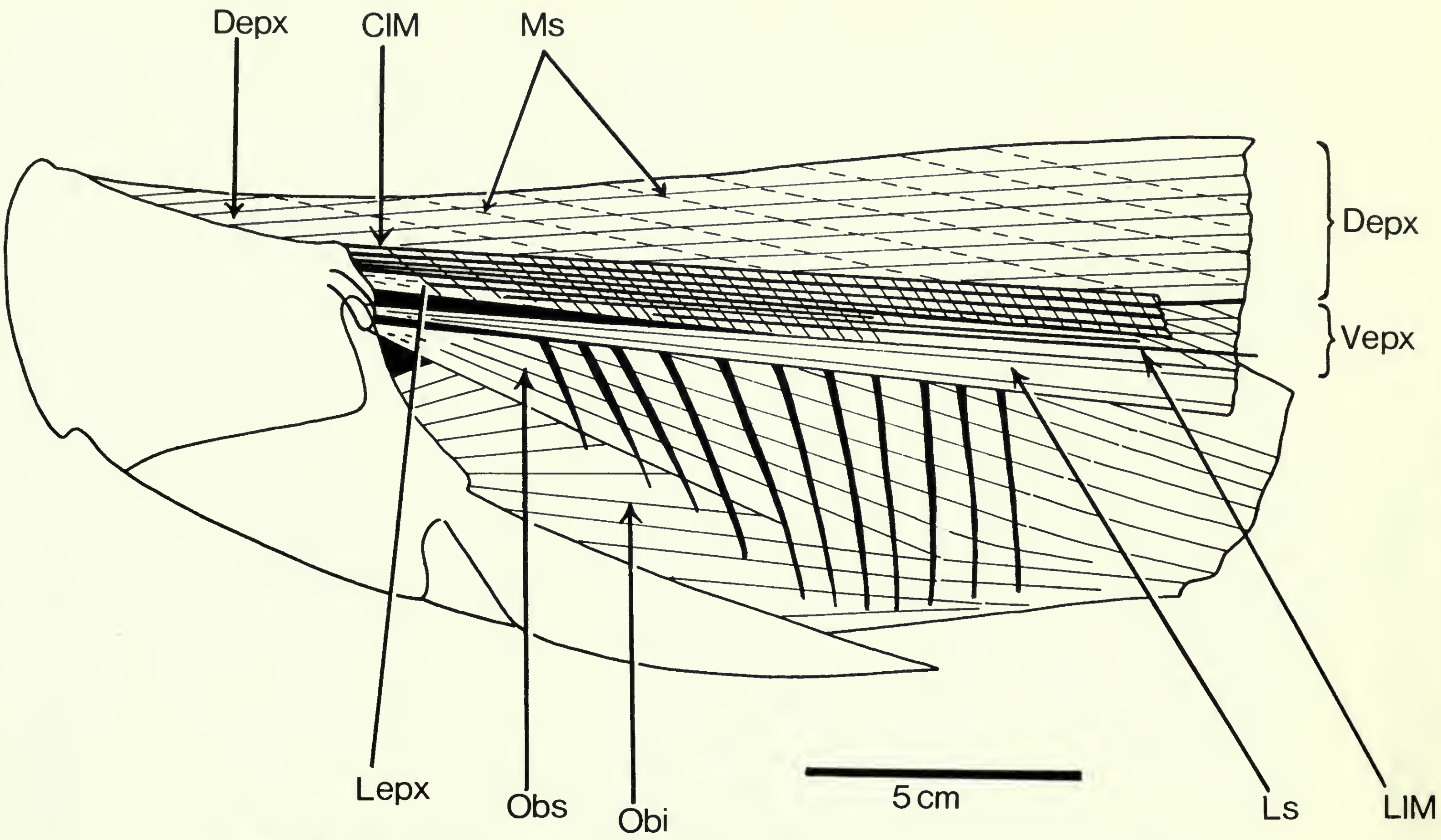
Depx
CIM
Ms
Depx
Vepx
Lepx
Obs
Obi
5 cm
Ls
LIM

Fig. 15 *Macrochirichthys macrochirus*, epaxial musculature. Lateral view, semi-diagrammatic.

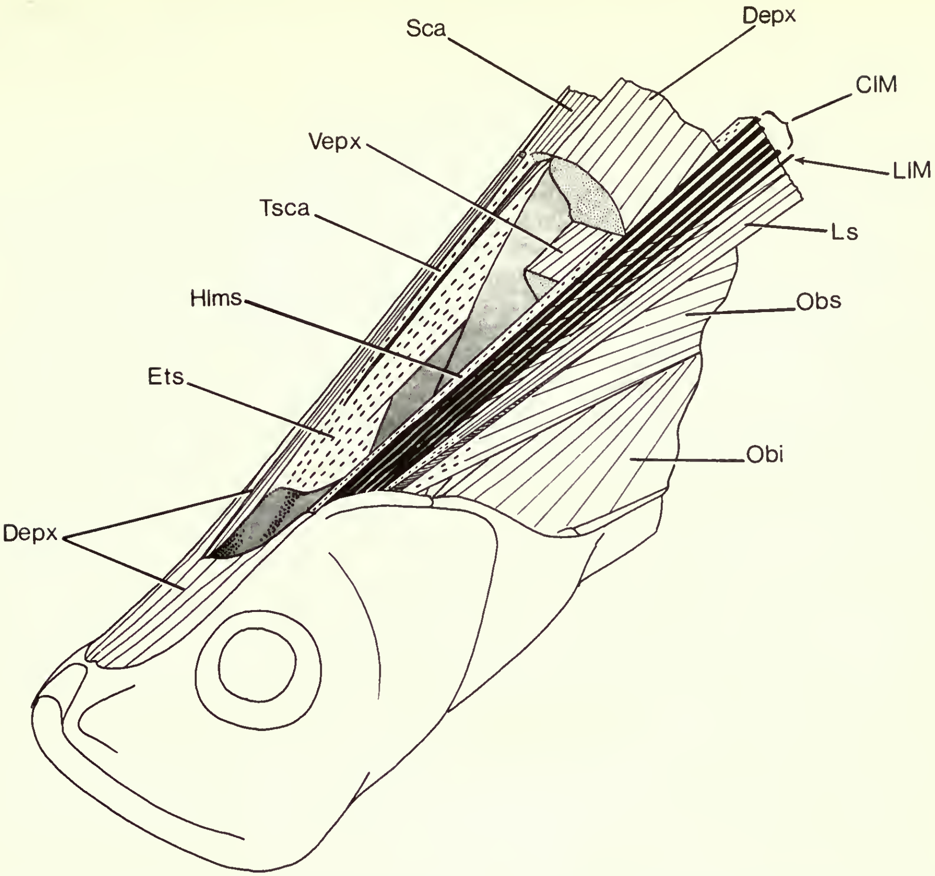

Fig. 16 *Macrochirichthys macrochirus.* Dorsal body musculature. Oblique dorso-lateral view, semi-diagrammatic. The epaxial musculature has been cut away; exposed parts of the skull and vertebral column are shaded.

The connection between the lower part of the *epaxialis* and the cranial intermuscular bone beam is a complex one and is shown semi-diagrammatically in Figs 17 & 18. The bones are connected to one another by an outer layer of widely spaced bands of muscle fibres orientated at angles of 40° to the horizontal (Lepx, Figs 15–18). Extending mesad from each bone is a thin horizontal myoseptum which separates layers of muscle fibres. In the top layer the fibres are directed toward the medial plane at the same angle as those in the overlying dorsal part of the *epaxialis.* Indeed, as mentioned above, the fibres of the two sections become merged and there is only a marginal myoseptum extending inward from the upper intermuscular bone. In each lower layer the fibres become more obliquely angled toward the medial plane, until those in the bottom layer strike the medial plane at 30–35° (Fig. 18). Thus, in a vertical section, the fibre arrangement is seen to follow a helical trajectory. Anteriorly, all the layers converge and terminate into tendinous bands which insert at the point of articulation of the intermuscular bone beam and the cranium.

The posterior tips of the cranial intermuscular bones are connected to the apices of those myomeres which form the posterior part of the *epaxialis.*

The *supracarinalis anterior* (Sca. Figs 16–18) originates from the first dorsal pterygiophore and extends forward as a broad band, triangular in cross-section, to a point above the neural complex. From there the muscle inserts into a thick tendon which at first runs dorsally to, and then eventually joins the midline septum (Ets, Fig. 16).

The *lateralis superficialis* muscle (Ls, Figs 15–18) is composed of three narrow bands of only a few fibres thickness. The medial surface of the *lateralis* is closely applied to the underlying *hypaxialis* and appears to be interlaced with fibres of that muscle. Anteriorly, the *lateralis* inserts *via* a thick tendon on to the upper part of the cleithrum.

The *hypaxialis* musculature is clearly divisible anteriorly as the *obliquus superioris* (Obs, Figs 15, 16 & 18) and the underlying *obliquus inferioris* (Obi, Figs 15, 16 & 18). The fibres of the *o. superioris* are directed at angles of 27–30° to the horizontal. Medially, insertion is by way of short segments (Hms, Fig. 17) plugging into the lower cavities of the centra. These segments are bordered ventrally by a broad tendon which extends between the posterior edge of the rib and its respective centra. Anteriorly, the fibres of the *o. superioris* insert *via* a thick tendon on to the upper part of the cleithrum, just below the insertion point of the *lateralis superficialis*.

The fibre direction of the anterior part of the *o. inferioris* varies from a 20° downward slope dorsally to a 10° upward slope ventrally. That part of the muscle running along the ventral margin of the body consists of rather widely spaced bands of tendinous fibres; the ventral edge, or keel, is a transluscent band of highly elastic connective tissue.

Beyond the pelvic fins the *epaxialis* and *hypaxialis* merge to form the typical teleostean pattern of zig-zag myomeres.

Comments and comparisons

Cranial intermuscular bones are developed to a greater or lesser degree in many cyprinids but are particularly well-developed in those genera with compressed, generally elongate bodies and obliquely aligned crania (see p. 171). Genera included in this category are: *Securicula*, *Salmostoma*, *Chela*, *Pseudolaubuca*, *Paralaubuca*, *Oxygaster* and *Pelecus*. In none of these, however, is there anything like the degree of cranial intermuscular bone (and associated epaxial muscle) development found in *Macrochirichthys*.

In *Securicula* there are four or five bones articulating with the posterior face of the cranium, but unlike the situation in *Macrochirichthys* they do not all articulate directly with the cranium but are attached to the epioccipital and supraoccipital by ligaments (Fig. 14A). Only the outer bone articulates with the epioccipital. A similar arrangement is found in other genera cited above, where again only the upper bone is firmly united to the cranium.

In *Salmostoma* the cranial intermuscular bones are weakly developed but tendinous bundles of the *epaxialis* run onto the epioccipital. No doubt ossification of these tendons has given rise to the situation found in *Macrochirichthys*.

With one exception all the genera noted above have short and markedly divergent cranial intermuscular bones unlike the horizontal bundles in *Macrochirichthys*. The exception is *Securicula* where the bones are long and diverge little from each other, approximating to the condition found in *Macrochirichthys*.

The functional significance of the cranial intermuscular bones, and the organization of the *epaxialis* is discussed on page 182.

Vertebral column (Figs 19–26)

The vertebral column in *Macrochirichthys* presents many interesting specializations. Not all the centra lie in the same horizontal plane, the dorsal surfaces of the 5th and 6th centra marking the highest point of the vertebral column. The 4th centrum is markedly sloped and serves as a 'step' to connect the lower level of the first three centra to the higher of the succeeding elements. From the 7th vertebra, the column slopes gently downward to the 18th or 19th centra where the axis is in the same horizontal plane as that of the first three centra (Fig. 19).

There are a total of 49–50 vertebrae (27 or 28 abdominal + 22 or 23 caudal excluding the fused $PU_1 + U_1$ elements); in one specimen there is a fusion of the 23rd, 24th and 25th centra.

The *first vertebra* (V1, Figs 20A–C) is small and ovoid in transverse section with a convex anterior face which articulates with the basioccipital socket. Short lateral processes are present on the upper part of the centrum. Antero-ventrally two small projections rest upon the anteriorly directed arms of the 2nd vertebra (see below). A pad of cartilage lies between each projection and its respective supporting arm.

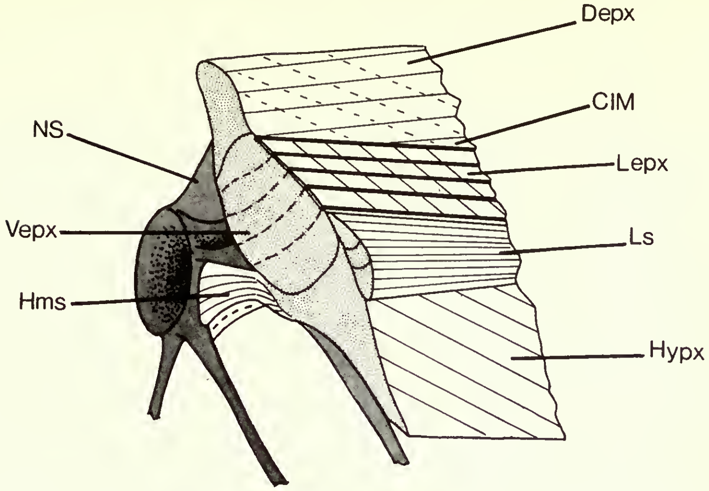

Fig. 17 *Macrochirichthys macrochirus.* Anterior oblique view of a transverse section through the dorsal body musculature. The section is taken at a point near the 8th vertebra. Skeletal elements are shaded.

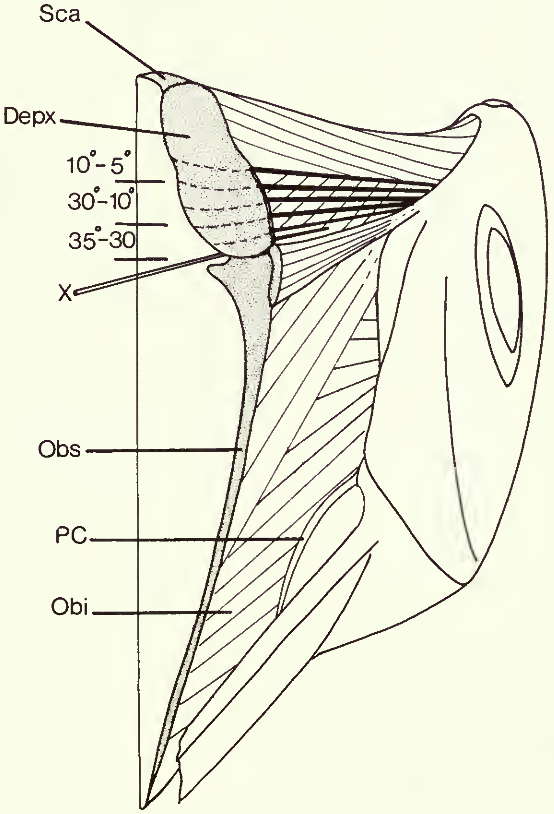

Fig. 18 *Macrochirichthys macrochirus.* Posterior oblique view of a transverse section through the body musculature. The axis of the vertebral column is indicated by ×. The horizontal myosepta of the ventral epaxial muscle are indicated by dashed lines. The angles made by the fibres with the median vertical plane are shown for each segment. The thick black lines represent the cranial intermuscular bones.

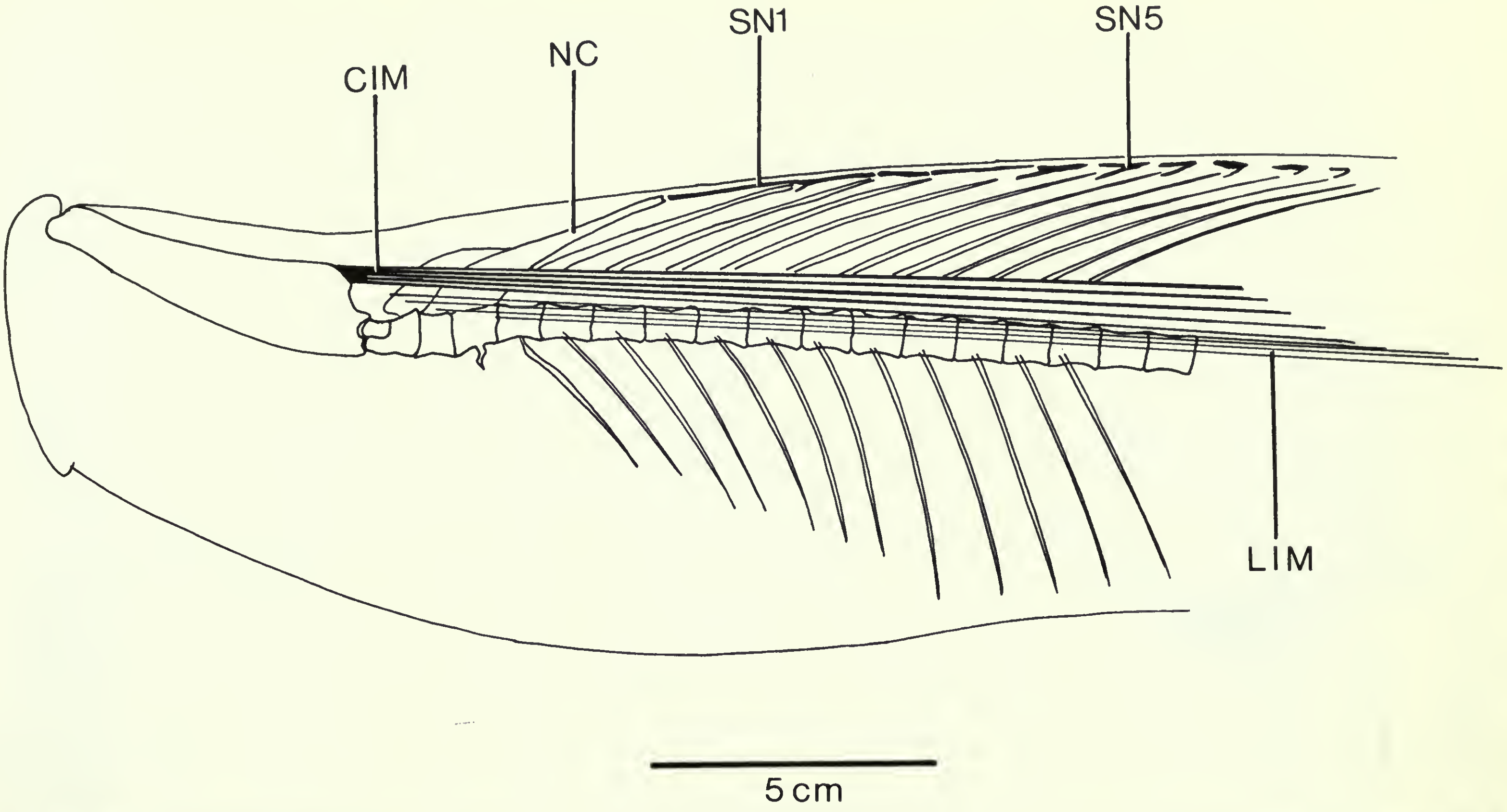

Fig. 19 *Macrochirichthys macrochirus.* Vertebral column, lateral view, semi-diagrammatic (drawn from a radiograph). Note upward slope of 4th centrum and downward inclination of the vertebral column.

The *2nd vertebra* is elongate, shaped anteriorly like the seat of an armchair (V2, Figs 20A–C). The seat itself is formed by two diverging arms, upon which rest the ventral projections of the 1st vertebra (see above). The centrum bears deep lateral processes, the anterior faces of which are slightly concave and articulate along their distal margins with the upper part of the cleithrum (see p. 177). Dorso-posteriorly each process extends caudad a thick spine.

The *3rd vertebra* (V3, Fig. 21B) is not fused with the 2nd and laterally carries the fossa in which the tripus articulates.

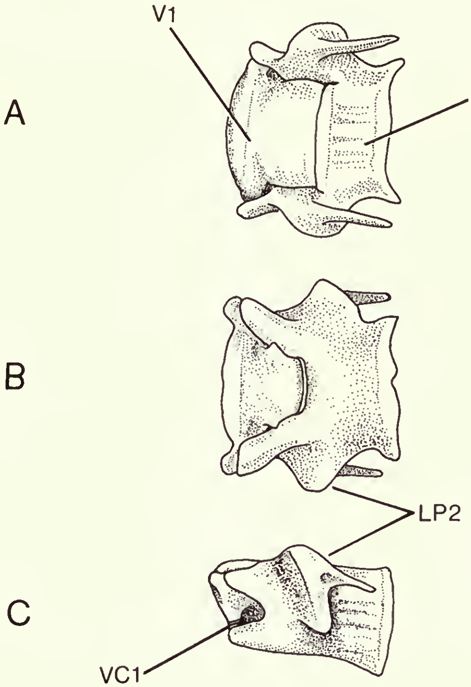

Fig. 20 *Macrochirichthys macrochirus*, 1st and 2nd vertebrae. A. Dorsal, B. Ventral and C. Lateral views.

The *4th vertebra* (V4, Fig 21B) bears lateral processes and the ossa suspensoria. The ventral surface of the centrum slopes upwards thus bringing its posterior face to the same level as the 5th and 6th centra which lie in a higher horizontal plane (see above).

The *second neural plate* (NP2, Fig. 21B) overlies the 1st and 2nd vertebrae. It is widely separated from the cranium. On either side, below its anterior border, lie the *claustra*, each of which articulates with the bowl of the ladle-shaped *scaphia*; in turn the stems of the scaphia articulate with the leading edge of the *third neural plate* (NP3, Fig. 21B). This large, broadly triangular bone covers the dorsal border of the 3rd centrum and overlies, but does not contact, the posterior half of the 2nd centrum. Extending from the posterior border of the third neural plate is the *neural complex* (NC, Fig. 21B) which is directed caudad at an angle of 20° to the vertebral column. Its posterior tip almost contacts a horizontally aligned supraneural. Basally the neural spine of the 4th vertebra contacts the neural complex, but halfway along its length is separated from this element. Distally it articulates with a fork of the first supraneural (SN1, Fig. 21B).

The neural spine of the 5th vertebra articulates distally with the anterior fork of the second supraneural (SN2, Fig. 21B). This supraneural extends horizontally over the sixth neural spine to contact the next rod-shaped supraneural lying between the sixth and seventh spines. From this point backwards a supraneural lies between each successive neural spine. However, the dorsal border of each supraneural becomes progressively less elongate until the bones have the form of a compressed nail (Fig. 19).

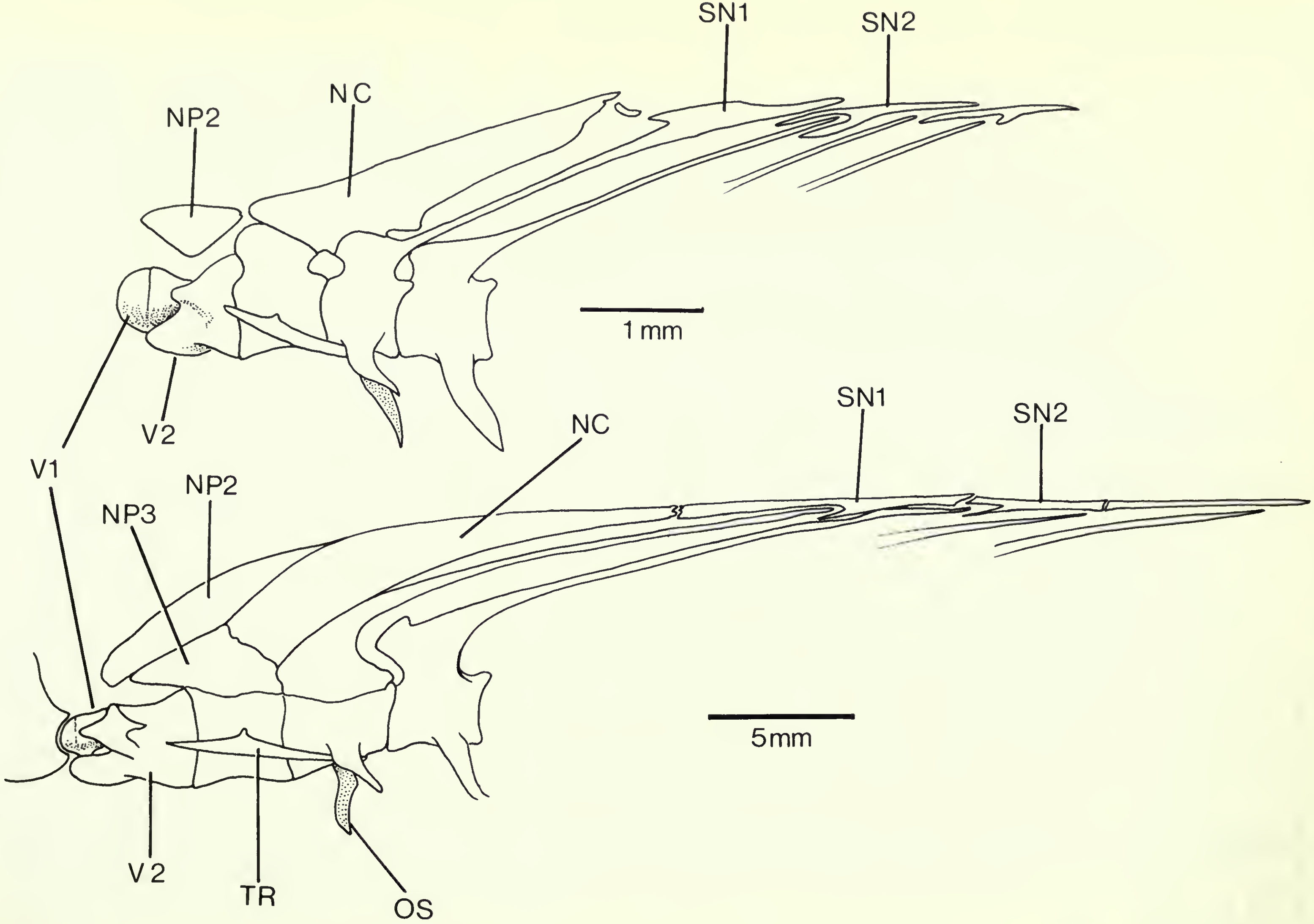
SN1
SN2
NC
NP2
1 mm
V1
V2
NC
SN1
SN2
NP2
NP3
5mm
V2
TR
OS

Fig. 21 *Macrochirichthys macrochirus*. Anterior vertebral column in A, a specimen of 30 mm SL, B, a specimen of 200 mm SL.

When the anterior elements of the vertebral column of the adult *Macrochirichthys* are compared with those of the juvenile, several differences are apparent.

In a juvenile of 30 mm SL the neural complex is a small triangular structure overlying the 1st and 2nd vertebrae (Fig. 21A). This is, in fact, the morphology of the second neural complex found in adults of other genera examined. The neural complex appears to be composed of two fused elements and is clearly separated from the fourth neural spine which is expanded distally as a lamellar plate. The 1st and 2nd vertebrae also differ from their adult condition. The 1st vertebra bears prominent forwardly directed lateral processes; similar but larger processes are also present on the 2nd vertebra (Fig. 22). It would appear that the processes of the 2nd vertebra grow forward and those of the 1st vertebra grow downward so that the 'cradle' of the adult is formed (see below).

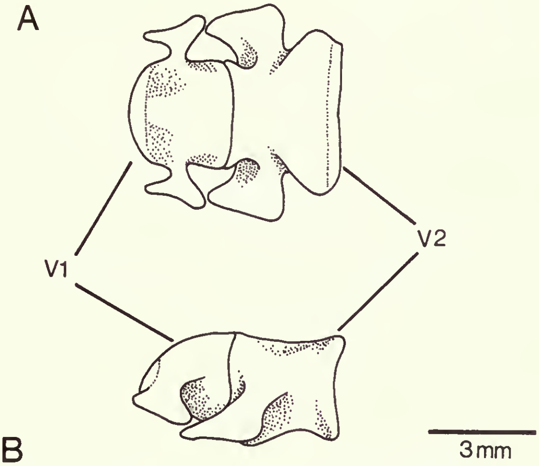

Fig. 22 *Macrochirichthys macrochirus*, 1st and 2nd vertebrae of a specimen 30 mm SL. A. Dorsal and B. Lateral view.

The sequence of changes that lead from the juvenile to the adult form are apparently as follows: the 2nd vertebra elongates, developing lateral and ventral processes; the anterior dorsal margin of the 3rd centrum grows forward to contact the first neural plate which, in turn, contacts and develops along the anterior border of the neural complex. The fourth neural spine expands anteriorly to unite with the posterior border of the neural complex; distally, the expanded portion of the fourth neural spine separates to become a supraneural which then grows forward to contact the neural complex.

Comments and comparisons

In an earlier paper (Howes, 1976) I drew attention to the peculiar arrangement of the dorsal elements in the vertebral column of *Macrochirichthys*. However, in figure 25 of that paper two anterior elements, comprising the neural complex, are mislabelled as neural spines, and the extent of the first vertebra is incorrectly indicated. I also remarked that the whole series of neural arches and supraneural elements forms an arc-like septum possibly serving to counteract stresses imposed by a presumed backward and upward movement of the cranium. It is now apparent that such a movement of the skull does occur (see p. 182) and that the type of articulation between the basioccipital and the first vertebra, coupled with the modifications to the 1st and 2nd vertebrae, serve to indicate the degree of movement possible (see p. 183).

Like *Macrochirichthys* the first centrum of *Securicula*, *Salmostoma*, *Oxygaster* and *Chela* is tapered anteriorly and presents a convex face articulating with the basioccipital (Figs 23A–C). Although in *Pelecus* the 1st vertebra has a rounded anterior face, it is not tapered. In other cyprinids the anterior face of the 1st centrum is flat or concave, a disc of cartilage being interposed between it and the basioccipital. All the genera mentioned above have a 1st vertebra with distally expanded lateral processes. In none has the 1st vertebra been modified to the extent it has in *Macrochirichthys*, but in some *Oxygaster* species there is a marked anterior extension of the lateral processes which thus resemble the condition found in the 2nd vertebra of the juvenile *Macrochirichthys* (Fig. 22 and p. 167). The lateral processes of the first vertebrae in *Securicula*, and *Salmostoma* are directed laterally but in *Chela laubuca*, although there is a pronounced lateral expansion of each process, the posterior border is curved and directed caudad to underlie the lateral process of the second vertebra. In *Chela maasi* and *C. caeruleostigmata* the distal margin of the lateral process of the first vertebra is considerably extended caudad; it is also closely united with the process of the 2nd vertebra to form a wide flange. The broad anterior edge of the first lateral process pivots against transverse expansions of the upper part of the cleithrum (see p. 183). (The information on these two species has been provided by Dr C. C. Lindsey.)

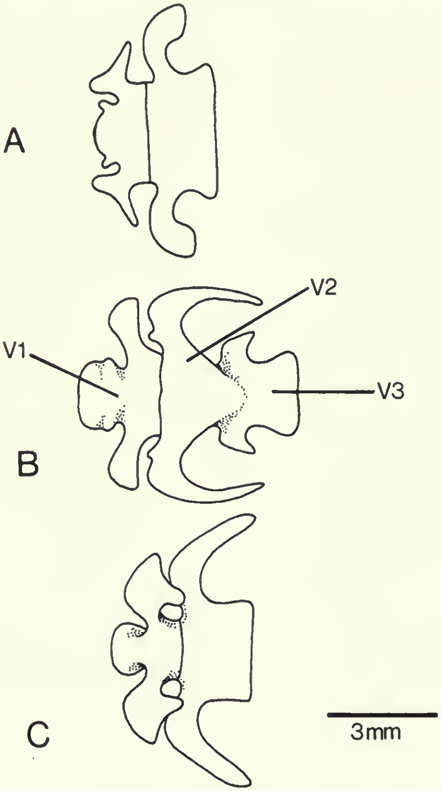

Fig. 23 1st and 2nd vertebrae of A. *Parachela oxygastroides* (dorsal view). B. *Securicula gora* (ventral view). C. *Chela laubuca* (ventral view). In *Securicula* the 2nd and 3rd centra are fused.

The 2nd and 3rd vertebrae are separated in *Chela*, *Oxygaster* and *Salmostoma* just as they are in *Macrochirichthys*, but in *Securicula* they are fused (Fig. 23B). Although fusion of the second and third elements appears to be the general condition in the cyprinids, there are genera, other than those mentioned above, in which they are separated (e.g. *Opsariichthys*, *Hemiculterella*, *Alburnus*). Whether this separation is indicative of a plesiomorph condition as suggested by Greenwood *et al.* (1966) can only be determined when relationships of these two centra are known for more genera. It does not appear to be of functional significance as is testified by its presence in *Macrochirichthys* and absence in *Securicula* and *Pelecus* which are almost all exactly alike in their gross cranial morphology.

The neural complex in *Securicula*, *Oxygaster* and *Salmostoma* has basically the same morphology as that described for *Macrochirichthys*.

In *Securicula* it is directed caudad at almost the same angle as in *Macrochirichthys* (30°) and is fused basally to the neural spine of the fourth vertebra (Fig. 24A). Distally, the fourth neural spine is expanded and contacts the neural complex; posteriorly its tip is forked and articulates with a supraneural The supraneurals are small, vertically aligned bones lying between each neural spine (Fig. 23).

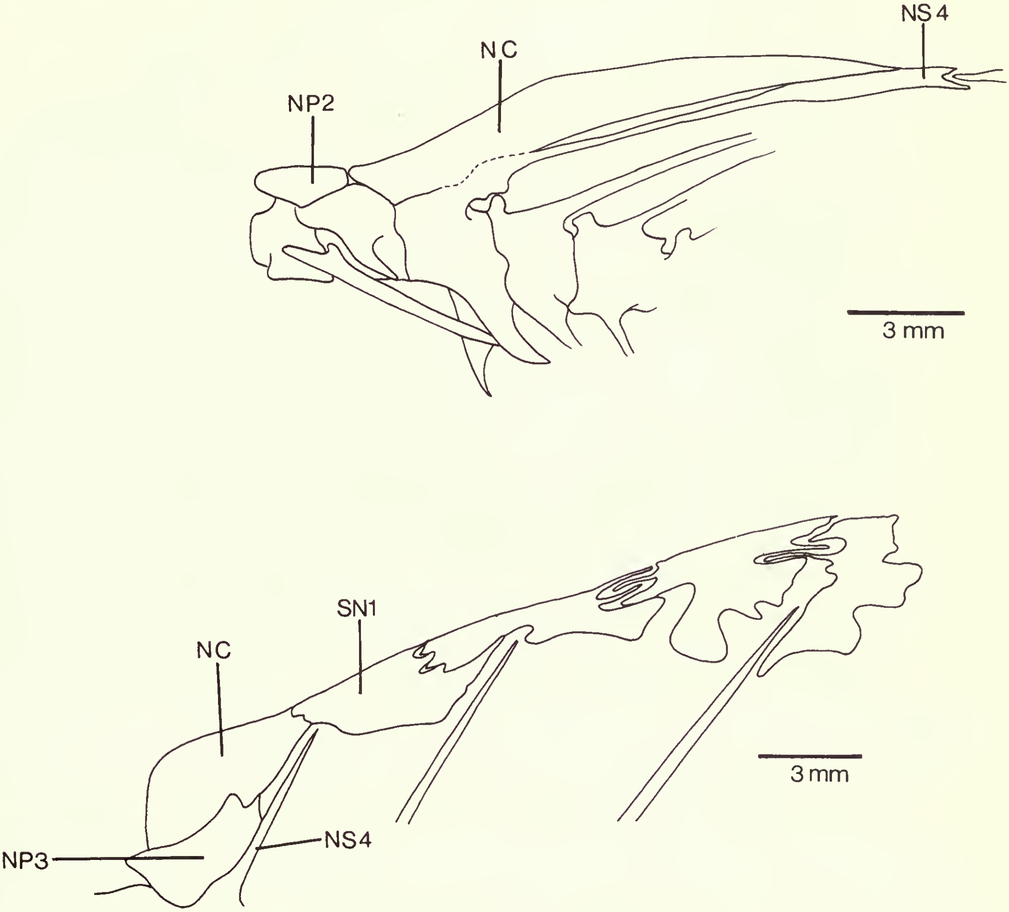

Fig. 24 Anterior vertebral column of A. *Securicula gora*, B. *Chela laubuca*.

Most species of *Oxygaster* display a similar arrangement between the neural complex and the supraneurals. As in *Macrochirichthys* the first two supraneurals are rod-like structures lying almost horizontally. However, in *Oxygaster anomalura* the anterior supraneurals are wide laminar bones and the neural complex does not contact the neural spine of the 4th vertebra as it does in its congeners (see p. 189 and Fig. 26B).

Salmostoma strongly resembles *Oxygaster anomalura* in the development of the supraneurals and in the angle at which the neural complex lies to the vertebral column (30° cf. 35° in *O. anomalura;* 40–45° in other *Oxygaster* species). The neural complex of *Salmostoma* is larger than in any of the genera previously mentioned.

In *Chela* there is a complex locking arrangement between the anterior supraneurals, none of which contacts the neural spines (Fig. 24B). The fourth neural spine does not contact the neural complex and is separated from it by the enlarged third neural plate (Fig. 24B).

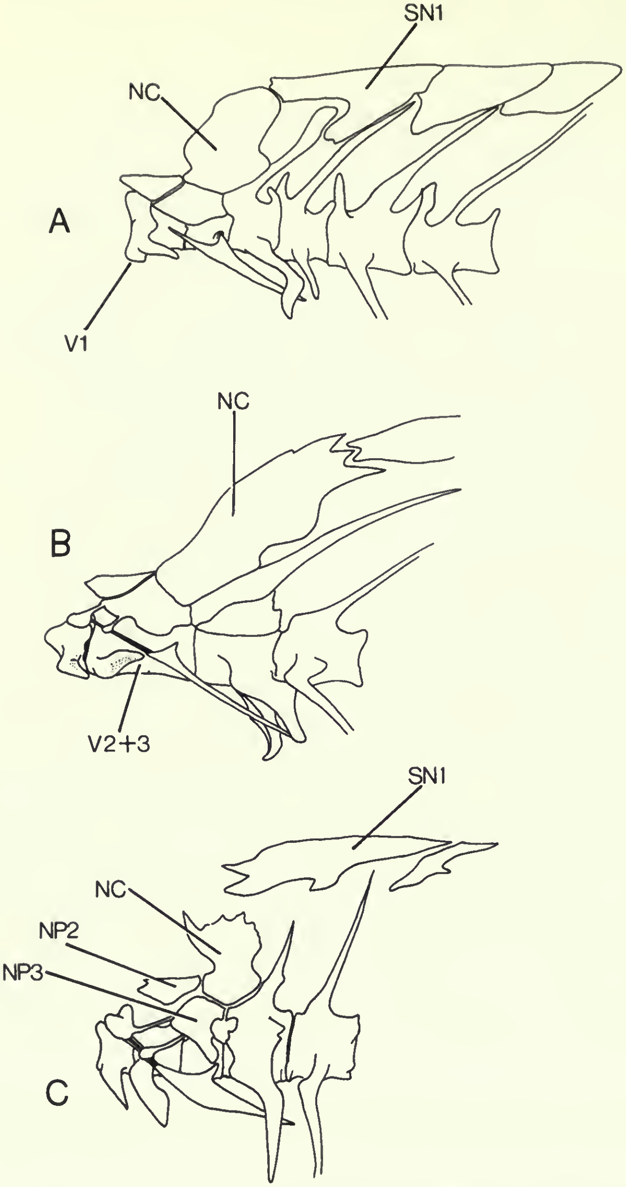

Fig. 25 Anterior vertebral column of A. *Pseudolaubuca sinensis* (2nd & 3rd centra separated ventrally but fused dorsally). B. *Pelecus cultratus* (2nd & 3rd centra fused). C. *Alburnus alburnus* (2nd & 3rd centra entirely separated).

Other genera currently assigned to the Cultrinae also possess hypertrophied supraneurals some of which articulate with neural spines. This arrangement is particularly well-developed in *Pseudolaubuca* where the supraneurals form a strong dorsal septum (Fig. 25A). A similar situation, but one developed to a lesser degree, is found in *Pelecus* (Fig. 25B) and *Paralaubuca*.

As mentioned above (p. 167), it appears that this arrangement of supraneurals and closely associated neural spines serves to combat stresses generated by the elastic movements of the myosepta extending between them. (See also p. 182).

In *Macrochirichthys*, *Securicula*, *Salmostoma*, *Oxygaster*, *Chela*, *Rasbora* and *Pelecus* the posterior face of the cranium is acutely inclined, and the supraoccipital process reduced or truncated. There is thus a wide space between the rear of the skull and the neural complex. This space is occupied by epaxial muscle and connective tissue (Fig. 26).

Most other cyprinid genera have a vertically aligned neural complex, most often extending forward so as to contact (e.g. *Labeo*, see Howes, 1978), or almost contact, the supraoccipital process.

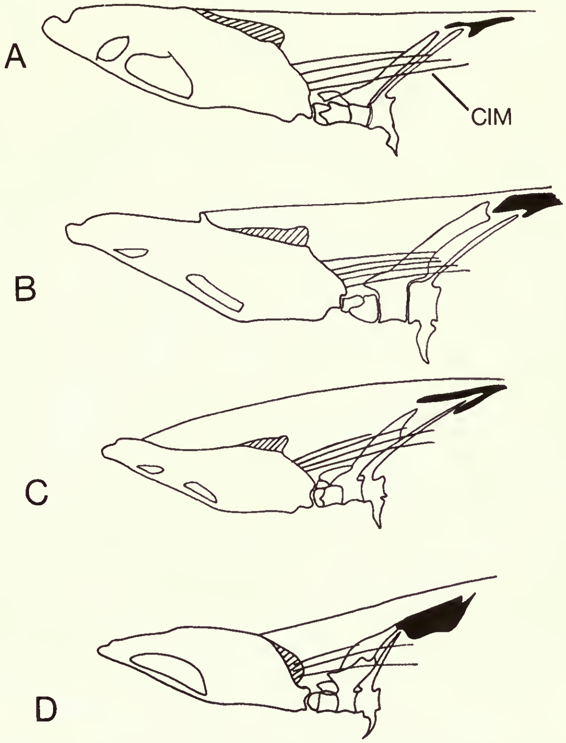

Fig. 26 Crania and anterior vertebral elements of A. *Salmostoma bacaila*. B. *Oxygaster anomalura*, C. *Parachela oxygastroides*, D. *Chela laubuca*. Supraoccipital process hatched, 1st supraneural shown in black. All drawn to same scale.

The angle at which the cranium is aligned to the vertebral column is undoubtedly of great adaptive significance in cyprinids. A shift in angle results in an equivalent reorientation of the jaws, which in the case of *Macrochirichthys* means that the jaws are almost vertical when the mouth is closed. In this fish the parasphenoid lies at an angle of 20° to the vertebral column and the posterior part of the cranial roof slopes backward at 10°. The same angles are measured in *Securicula* and *Pelecus*; as in *Macrochirichthys*, it is only the posterior (post-parietal) part of the cranium that slopes, anteriorly it is almost horizontal. The same angles are again found in *Oxygaster anomalura* but here the cranial roof has a continuous slope broken only by the raised parietal ridges (see p. 172 and Fig. 26B). Other *Oxygaster* species have the parasphenoid aligned at an angle of 20–25° (the same as the anterior part of the cranial roof, Fig. 26C). The parasphenoid in *Salmostoma* lies at 20° to the vertebral column and the cranial roof at 25°; as in *Macrochirichthys* and *Securicula* it is only the post-parietal part of the cranium that is sloped (Fig. 26A).

The dorsal profile of the cranium in *Chela* is convex, with a marked posterior slope, the supraoccipital being confined entirely to the posterior part of the skull. The parasphenoid lies at 20° to the vertebral column, an angle no greater than in the other genera considered; but the epaxial musculature makes an oblique angle with the cranium whereas in the other examples it lies almost horizontally. Apart, that is, from those *Oxygaster* species in which the musculature has extended to the anterior part of the skull (Fig. 26D).

Mention was made above of the parietal ridges in *Oxygaster anomalura* and of the difference between this and other *Oxygaster* species in the angle formed between the cranial roof and the vertebral column. Only a slight change in this orientation would enable the epaxial musculature to extend further forward, with a consequent reduction and finally a complete disappearance of the parietal ridge. This may well have been the transformation sequence from the ancestral form to the derived species of *Oxygaster* (see p. 189).

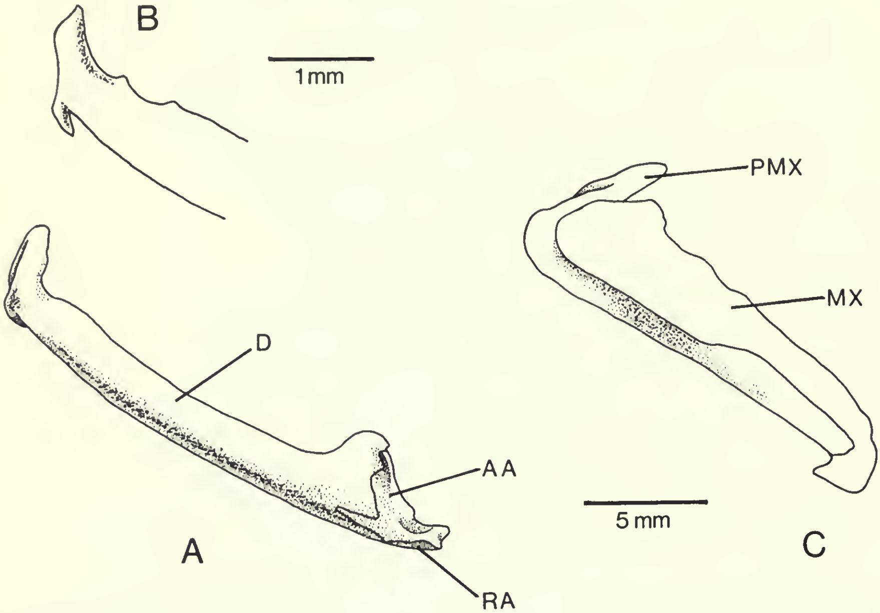

Fig. 27 *Macrochirichthys macrochirus* jaw bones. A. Lower jaw. B. Anterior dentary of a specimen 30 mm SL. C. Upper jaw. Lateral views.

Jaws (Figs 27–29)

The *premaxillae* of *Macrochirichthys* are long thin bones with short triangular ascending processes (Fig. 27C). Each ascending process curves mesad to meet its fellow along the midline; contact is effected by a socket joint, the faces of one side being raised to fit into an elongate groove in the face of the other (Fig. 28). The separation of the ventral leading edges of the premaxillae by this type of joint enables the prominent tip of the lower jaw to be accommodated when the mouth is closed.

The *maxilla* is expanded anteriorly. Its ventral border is rounded and overlaps the premaxilla for half of that bone's length; beyond this point it lies along the top of the premaxilla. Anteriorly, the ventral medial process, which overlaps the inner side of the premaxilla, widens and is linked with its partner by a thick ligament.

The *dentary* (Fig. 27A) is shallow, its anterior tip produced into a high, mallet-like process. Lying posterior to this process is a deep notch. In a juvenile specimen (30 mm SL) the symphysial process is produced ventrally as well as dorsally and there are two shallow notches (Fig. 27B). The coronoid process of the lower jaw is shallow and is formed partly from the dentary and partly from the anguloarticular. The posterior margin of the coronoid process (anguloarticular) is bent outward as a narrow flange and provides an insertion area for the tendon of *adductor mandibulae* A_2 muscle.

Comments and comparisons

When the mouth of *Macrochirichthys* is closed the kinethmoid lies in the anterior cavity of the ethmoid block, and the symphysial process of the lower jaw lies between the premaxillaries. As the lower jaw moves downward, protrusion of the upper jaw is effected by the forward rotation of the kinethmoid pushing the premaxillaries forward (Fig. 29).

The marked upper jaw protrusion seen in most other cyprinids (Alexander, 1966) is lost in *Macrochirichthys*, because of the direct connection between the kinethmoid and the premaxillaries. In the majority of cyprinid genera the kinethmoid is connected to the premaxillaries by a long ligament which enables the necessary protrusion.

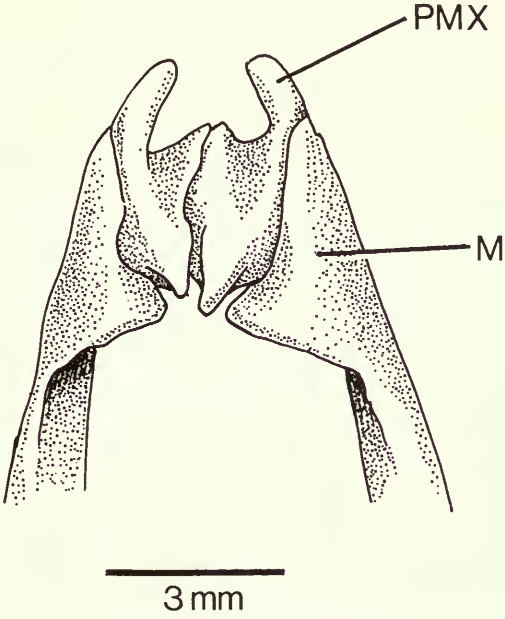

Fig. 28 *Macrochirichthys macrochirus*, dorsal view of upper jaws.

The jaws of *Securicula* are shorter than those of *Macrochirichthys* but the dentary is deeper and the coronoid process is not set so far posteriorly; the process is formed entirely from the dentary, the anguloarticular meeting it at a shallow angle and presenting a long dorsal border. The symphysial process, however, is well-developed and is followed by a pronounced cavity in the upper margin of the dentary. *Salmostoma* has an almost identical jaw morphology.

Only *Oxygaster* has the same kind of premaxillary socket joint as *Macrochirichthys* (see p. 185).

Various types of cyprinid jaw have been discussed in an earlier paper (Howes, 1978) where it was suggested that those species with elongate jaws lack the degree of protrusibility of the shorter jawed species, a condition exemplified by *Macrochirichthys*.

In *Chela* the upper jaw is protractile, although not to the degree seen in some barbine or leuciscine genera; the lower jaw is shallow and widely curved mesad. The gape is large and when opened the mouth is almost circular. The functional significance of this type of mouth is considered on p. 184.

Suspensorium and associated musculature (Figs 30–32)

The *hyomandibula* of *Macrochirichthys* has a wide lateral face which bears a large fossa, the ventral border of which projects anteriorly as a small laminar process (HMP, Fig. 30A). This cavity provides the site of attachment for the *levator arcus palatini* muscle. A description of this muscle was given in a previous paper (Howes, 1976 : 242, fig. 24) where it was noted that the element is divided, the outer part inserting onto the small lateral process. The lower limb of the hyomandibula is directed forward at an angle of 45° from the vertical.

The *metapterygoid* and *entopterygoid* are extensive bones (Fig 30A). The metapterygoid joins, and slightly overlaps, the limb of the hyomandibula. Its lateral face provides a site for the attachment of the small *adductor arcus palatini* muscle. A fibrous sheet of connective tissue extends from the palatine to the lateral faces of the metapterygoid and entopterygoid (see fig. 23 in Howes, 1976).

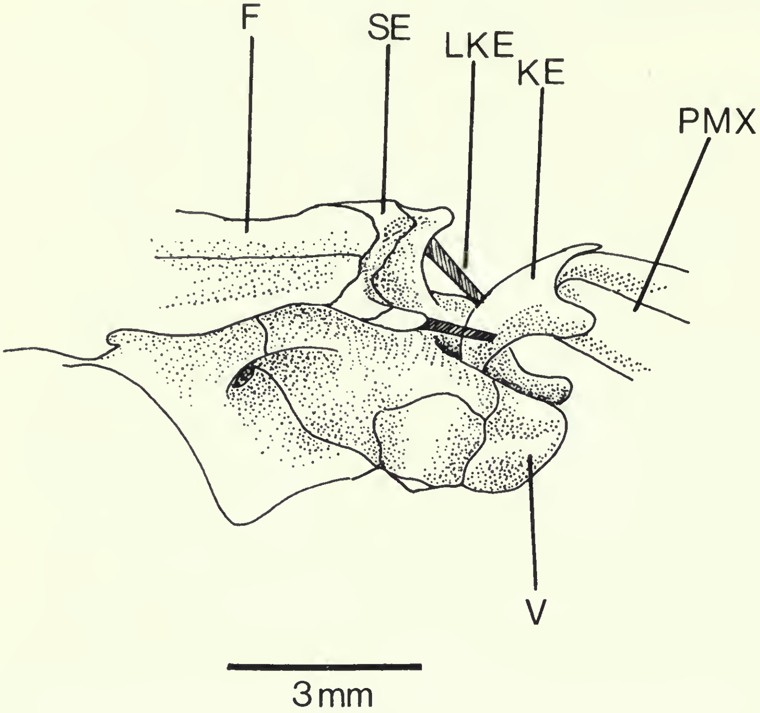

Fig. 29 *Macrochirichthys macrochirus*, ethmoid-jaw connection. Dorso-lateral view.

The *ectopterygoid* is long and narrow and has a wide union with the palatine. The *autopalatine* itself is thick and has a long medial process articulating with the ethmoid.

The *quadrate* contains a small foramen situated just posterior to the articular condyle (QF, Fig. 30A).

The quadrate together with the metapterygoid and symplectic border a fenestra in the suspensorium (MQF, Fig. 30A).

Comments and comparisons

The only other genus presently included in the Cultrinae which has a lateral process on the hyomandibula is *Pseudolaubuca*. In this case it serves the same function as the process in *Macrochirichthys*, namely, as an insertion point for a divided *levator arcus palatini* muscle. In *Securicula* the hyomandibula is narrower than that of *Macrochirichthys* and the ventral limb is vertically aligned (Fig. 30B). There is only a slight indication of a lateral depression. The metapterygoid joins the hyomandibula halfway along the ventral limb of the later, which it overlaps laterally. The *levator arcus palatini* is divided in *Macrochirichthys*, but the inner section of the muscle inserts on the hyomandibula and the outer on the metapterygoid (Figs 31A & B). The suspensorial fenestra is larger than in *Macrochirichthys* and the dorsal edge of the symplectic provides the entire lower border of the fenestra. There is a large quadrate foramen present (Fig. 30B).

The metapterygoid-quadrate fenestra has been commented upon and its functional significance discussed in *Macrochirichthys* in an earlier paper (Howes, 1978). It may be added here that in addition to *Opsariichthys*, *Zacco* and *Macrochirichthys* this fenestra is also recorded in *Securicula*

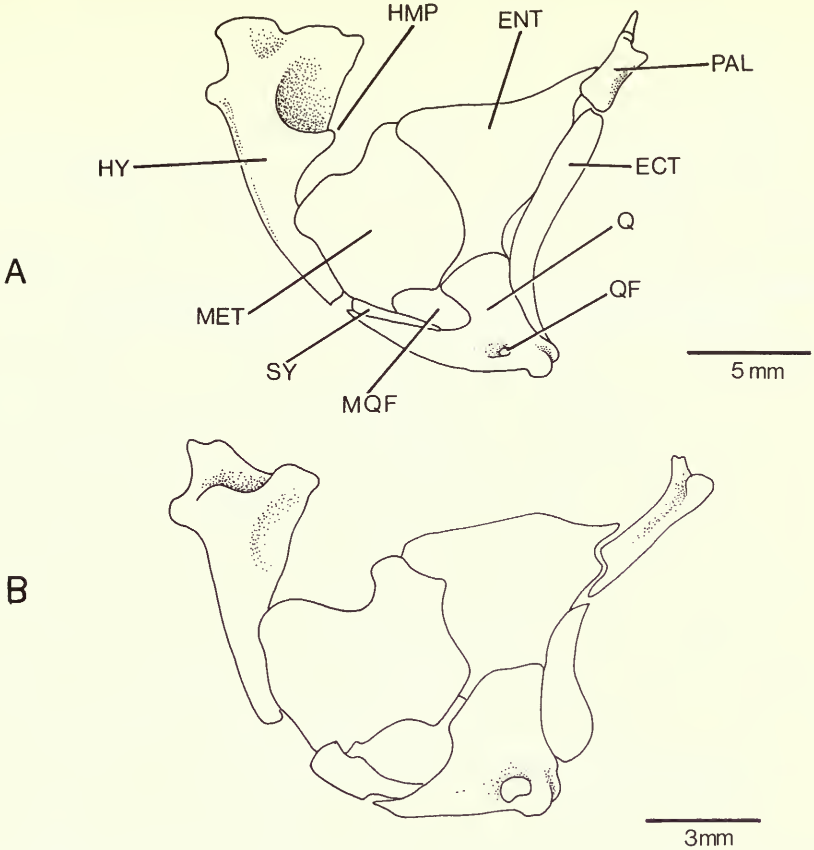

Fig. 30 Hyopalatine arch in lateral view of A. *Macrochirichthys macrochirus*, B. *Securicula gora.*

(=*Pseudoxygaster*), *Salmostoma* (Mirza, Alam & Kausar, 1974), *Aspidoparia* (p. 192) and *Luciosoma* (pers. obs.). When comparing the various *Salmostoma* species one encounters a situation like that existing between *Macrochirichthys* and *Securicula*, namely that with a lengthening and near vertical orientation of the jaws there is a reduction in size of the fenestra and a reduction in length but deepening of the symplectic (cf. *Salmostoma sardinella* – a short-jawed

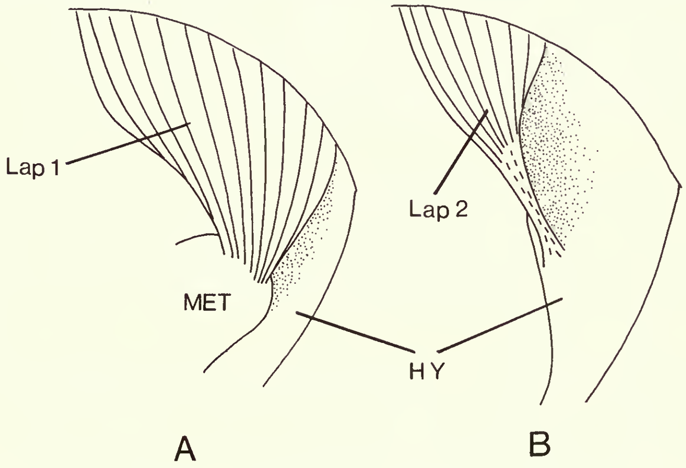

Fig. 31 *Securicula gora, levator arcus palatini* muscle. A. Outer aspect. B. Inner layer.

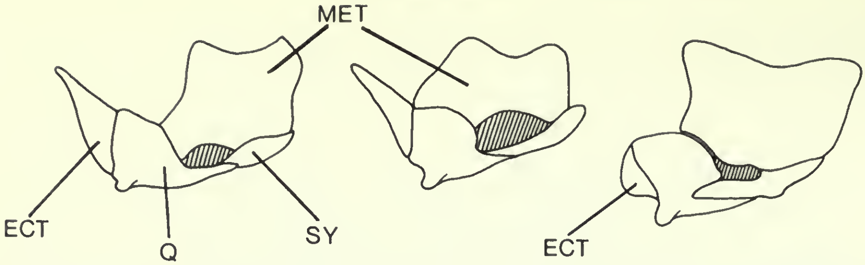
MET
ECT
Q
SY
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Fig. 32 Pterygoid bones of A. *Salmostoma sardinella*, B. *Salmostoma bacaila*. C. *Aspidoparia mora*. Metapterygoid-quadrate fenestra hatched. All drawn to same scale.

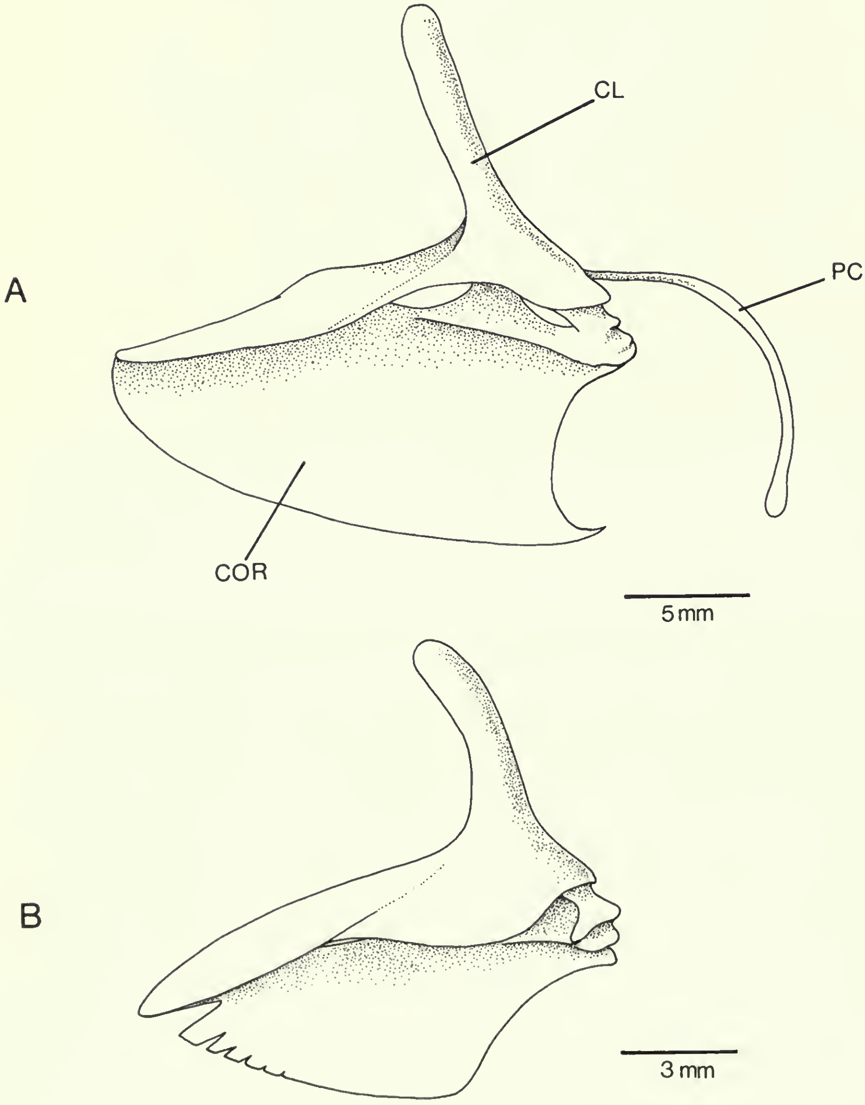
A
CL
PC
COR
5 mm
B
3 mm

Fig. 33 Pectoral girdles in lateral view of A. *Macrochirichthys macrochirus*, B. *Securicula gora*.

species, and *S. baicala* – a long-jawed species, Figs 32A–C). It is interesting to note that in *Aspidoparia*, although the fenestra is greatly reduced, it appears to be the result of a partially reversed trend, i.e. a shortening of the lower jaw combined with its near vertical orientation (Fig. 32C). Along with earlier authors I had considered this fenestra as a plesiomorph character for the cyprinids (Howes, 1978), an assumption which I think is borne out by the condition of this feature in *Salmostoma*, a taxon I have reason to believe is the plesiomorph member of the group under discussion (see p. 186).

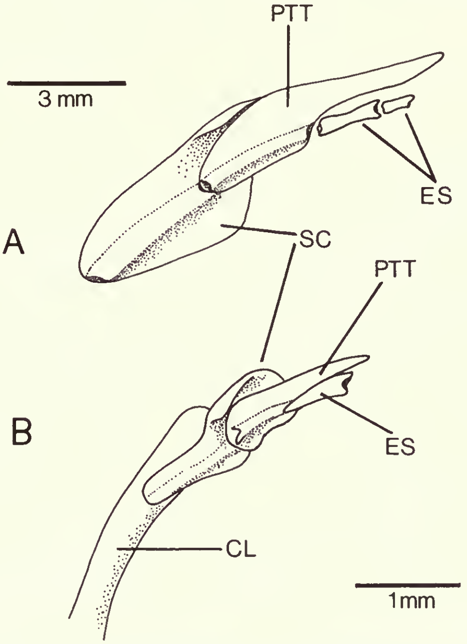

Fig. 34 *Macrochirichthys macrochirus*, supracleithrum, posttemporal and extrascapular. A. Adult, B. Juvenile (30 mm SL).

Pectoral girdle and associated cranial bones (Figs 33–36)
The upper limb of the *cleithrum* in *Macrochirichthys* is short and columnar, sloping forward at an angle of 45° to the vertical. The upper part of the medial face bears a narrow process which is attached by a thick ligament to the anterior face of the transverse process of the 2nd vertebra (see p. 165). The lower cleithral limb slopes anteriorly at 45° from the vertebral axis. This lower part is long and its anterior tip comes to lie below the posterior part of the orbit (Fig. 33A).

The *coracoids* are extensive and contact each other along their medial faces. The posterior border of each coracoid is markedly concave and the ventral border extends backwards to a point below the pectoral fin.

The *supracleithrum* (SC, Fig. 34) is a broad, triangular bone, its anterior dorsal border curved laterally to overlie the edge of the posttemporal. The sensory canal runs along the middle of the supracleithral face. The *posttemporal* is cleaver-shaped, its posterior border rounded, the sensory canal running close to its lower border (PT, Figs 34A & B). Along the antero-ventral border of the posttemporal lies the *extrascapular* which may sometimes be fragmented into two elements (ES, Figs 34A & B).

In a juvenile specimen (30 mm SL) the supracleithrum is a squared S-shaped bone with a well-developed dorso-lateral flange; the posttemporal has a more rounded posterior border and the extrascapular is in contact with the ventral border of the posttemporal (Fig. 34B).

The *postcleithrum* of the adult is extremely long and is curved ventromesially, its dorsal tip lying at the same level as the posteroventral tip of the coracoid (Fig. 33A).

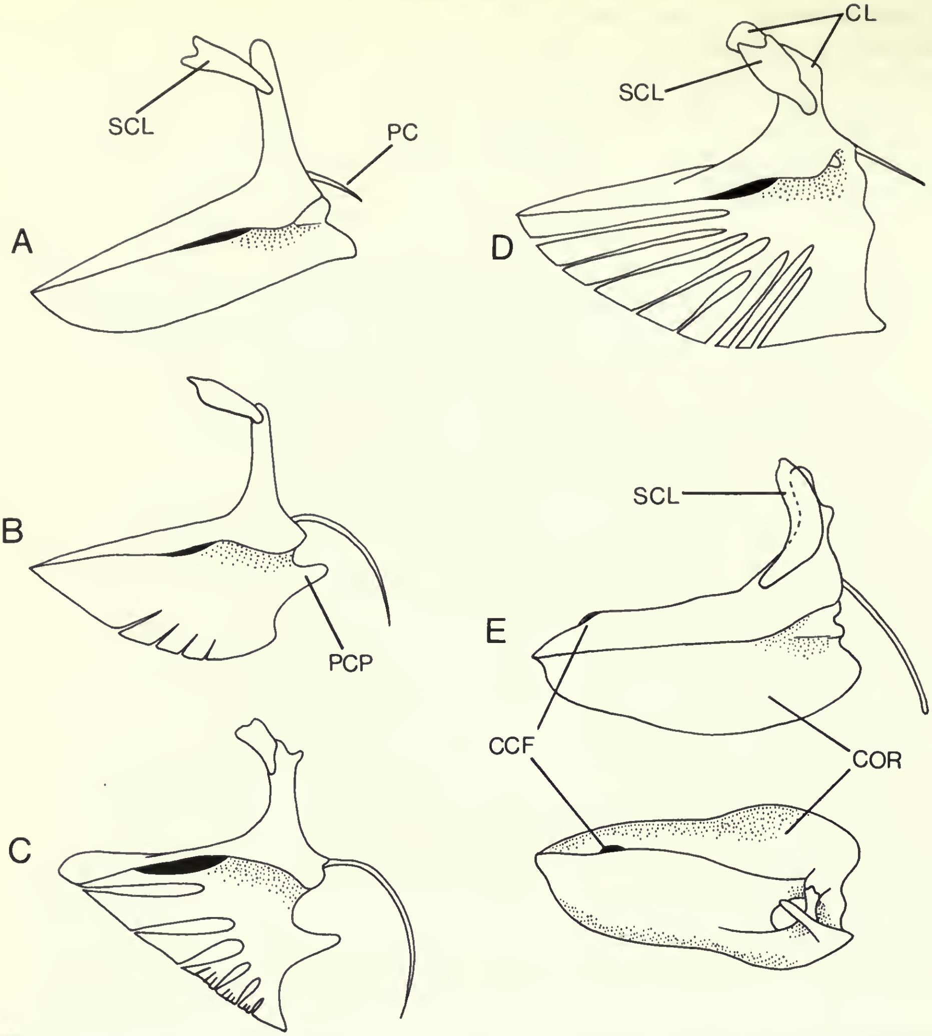

Fig. 35 Pectoral girdles of A. *Salmostoma bacaila*, B. *Oxygaster anomalura*, C. *Parachela oxygastroides*, D. *Pelecus cultratus*, E. *Chela laubuca* in lateral and F. Dorsal view.

Comments and comparisons

Large pectoral fins with a correlated expansion of the coracoids appear to be characters shared by many genera currently assigned to the Cultrinae. However, the morphology of the pectoral girdle differs significantly amongst these genera. The short, anteriorly inclined upright limb of the cleithrum in *Macrochirichthys* and *Securicula* is columnar (Figs 33A & B), whereas in *Oxygaster*, *Salmostoma* and *Chela* it is lamellar (Figs 35A, B, C & D). In other cultrine genera (apart from *Pelecus;* see below) the limb is long and vertically aligned, and the lamellar border is extended posteriorly, a condition typical for the majority of cyprinids. In *Pelecus*, although the upright part of the cleithrum is short and slopes forward, it is broadly lamellar and the supracleithrum articulates halfway along its length instead of ioining the cleithrum at its dorsal point as it does in *Macrochirichthys* and the other genera cited above (Fig 35D).

The supracleithrum in *Oxygaster* is broad, and in *O. anomalura* has a slight lateral lip overlying the depression in which the posttemporal articulates (Fig. 36A). The posttemporal in this species is elongate and has the same shape as that of *Macrochirichthys*, whereas in other species of *Oxygaster* the bone is short and curved sharply forward. In all species of *Oxygaster* the sensory canal runs close to the posterior border of the bone. The extrascapular of *O. anomalura* is elongate with an upwardly curved anterior tip, and again it more closely resembles its counterpart in *Macrochirichthys* than that of the other *Oxygaster* species.

The supracleithrum in *Salmostoma* is narrowly triangular, the sensory canal running along the middle; the posttemporal is wide and lacks an indented ventral border. The extrascapular too is triangular and partly overlies the anterior margin of the posttemporal (Fig. 36D). Although the supracleithrum and posttemporal in *Securicula* are wider and shorter than those of *Salmostoma* they share the same characteristics and likewise the extrascapular lies at the centre and overlaps the anterior border of the posttemporal (Fig. 36C).

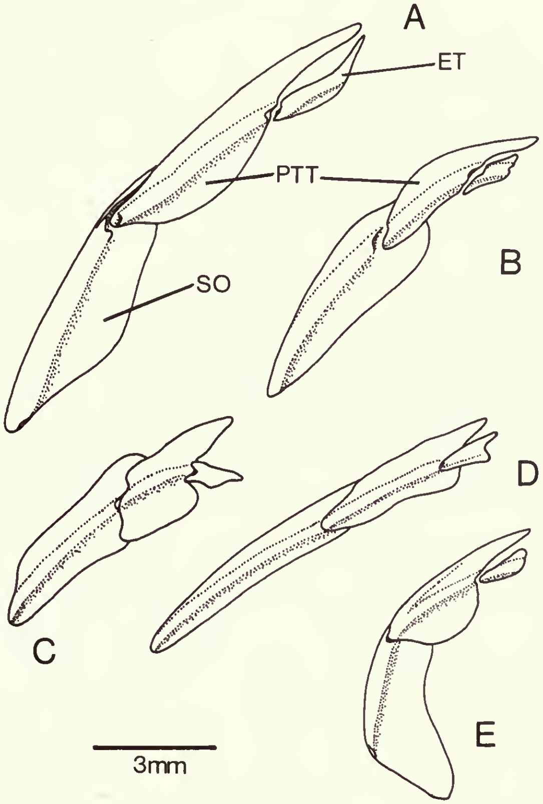

Fig. 36 Supracleithrum, posttemporal and extrascapular in A. *Oxygaster anomalura*. B. *Parachela oxygastroides*. C. *Securicula gora*. D. *Salmostoma sardinella*. E. *Chela laubuca*.

In *Chela* the supracleithrum is extensive, its anterior border extending downward to almost the lower part of the cleithrum (Figs 35E & 34E). The shape of the posttemporal and of the extrascapular more nearly resembles *Oxygaster anomalura* than any other taxon. A notable feature of the pectoral girdle of *Chela* is the medial extension of the upper part of the cleithrum. This part of the cleithrum contacts the leading edge of the transverse process of the first vertebra, similar to the situation in *Macrochirichthys* (see above). In *Chela maassi* the medial cleithral extensions are most extensive and appear to act as part of a pivot for the cranium against the vertebral column (information supplied by Dr C. C. Lindsey; see also p. 184). The coracoids are not greatly extended and are widely divergent.

There is much variation in the degree of development of the coracoids, which are most extensive in *Macrochirichthys*, *Securicula* and *Pelecus*. In *Securicula* as in *Macrochirichthys* the medial faces of the coracoids are in contact over most of their length but lack the posteroventral extension found in that genus; in this respect, but not in their greater depth, they more closely resemble the coracoids of *Salmostoma* (cf. Figs 33B & 35A). A prolongation of the posterior coracoid border is present in all *Oxygaster* species but in this genus it takes the form of a midlateral rather than a posteroventral extension. In *Pelecus* the coracoid border is concave, and in other cultrines it is straight or rounded. The ventral coracoid border is deeply incised in all *Oxygaster* species being most marked in *O. hypophthalmus*, and weakest in *O. anomalura* (Figs 35B & C). A weakly incised border is also found in the coracoid of *Securicula* (Fig. 33B), and there is some indentation in a juvenile *Macrochirichthys* (30 mm SL) but no sign of this exists in any adult specimens I have examined. Sorescu (1968) notes and figures an incised coracoid in *Macrochirichthys*; unfortunately she did not state the size of the specimen examined.

An incised coracoid is present in *Pelecus* (noted and figured by Rauther, 1950 and Sorescu, 1968). Here, however, the indentations are narrow and finger-like, thus quite unlike the wide almost triangular or ellipsoidal indentations of the genera cited above (Fig. 35D).

The only other cyprinid in which I have found an irregularity of the coracoid ventral border is *Alburnus*, in which it is serrated.

An indented coracoid possibly has some functional association with the way in which the pectoral fins are extended and rapidly jerked forwards (see p. 183). In passing it may be noted that in some characoids which have extensive coracoids (*Gasteropelecus*, *Thoracocharax*), the bones bear deep grooves which provide attachment for tendons supporting bundles of the *adductores superficialis* muscle. In the cyprinids the indentations are covered by a tendinous fascia and in both cases the channeling of the coracoids possibly provides a reduction in weight, an increased area for muscle attachment (in the characoids), and possibly a shock-absorbent system (in the cyprinids).

In all other genera placed in the Cultrinae the coracoids are not in contact along their medial faces, and diverge from one another to varying extents; all have a large fenestra between the coracoid and the cleithrum (anterior fenestra of Brousseau, 1976). In *Chela* the anterior fenestra is reduced in size or may be completely absent (Fig. 35E). Although a fenestra is present in *Rasbora* it shows considerable interspecific variation in size, in some species being reduced to a minute opening and in others confined to the coracoid. A similar situation occurs in *Danio*. As in *Rasbora* the anterior fenestra is absent, but the foramen is developed in the high anterior crest of the medial dorsal ridge of the cleithrum (ventral cleithral lamina of Brousseau, 1976).

Mesially curved, elongate postcleithra, like those of *Macrochirichthys* are found in all *Oxygaster* species. Postcleithra are absent in *Securicula* and are reduced to short straight bones in *Salmostoma*. In other cultrines the postcleithra vary from being long and curved in *Culter* and *Erythroculter* (although never forming a wide arc as in *Oxygaster* and *Macrochirichthys*) to short and straight in *Pelecus*.

The abdominal keel and scale rows (Figs 37 & 38).

The ventral surface of the abdomen of *Macrochirichthys* is greatly compressed, with a knife-like edge. The scales do not overlap along the ventral midline, with the result that the skin is exposed medially below the lowest row of scales. The exposed skin is translucent and pervaded by oblique strands of tendinous tissue.

Above and around the pectoral fin origin the skin is loose and the scale rows broadly overlap. When the pectoral fins are moved downwards and rotated forward the skin is taught and the scale rows become vertically aligned with hardly any overlap (Figs 37A & B). There is no pectoral axial scale.

Comments and comparisons

The presence of a ventral keel has been a major diagnostic feature in defining the subfamily Cultrinae and the extent to which it is developed has been used in delimiting certain cultrine genera (see, for example, pages 194–195).

Most cyprinid fishes with laterally compressed bodies have the abdomen keeled along the midline (e.g. *Nematabramis*, *Chelaethiops*), the keel being formed by overlapping of the scale rows. The sharpness of the keel varies, and its longitudinal extent is often difficult to determine. Specimens of various cultrines I have examined show that the development of the keel varies

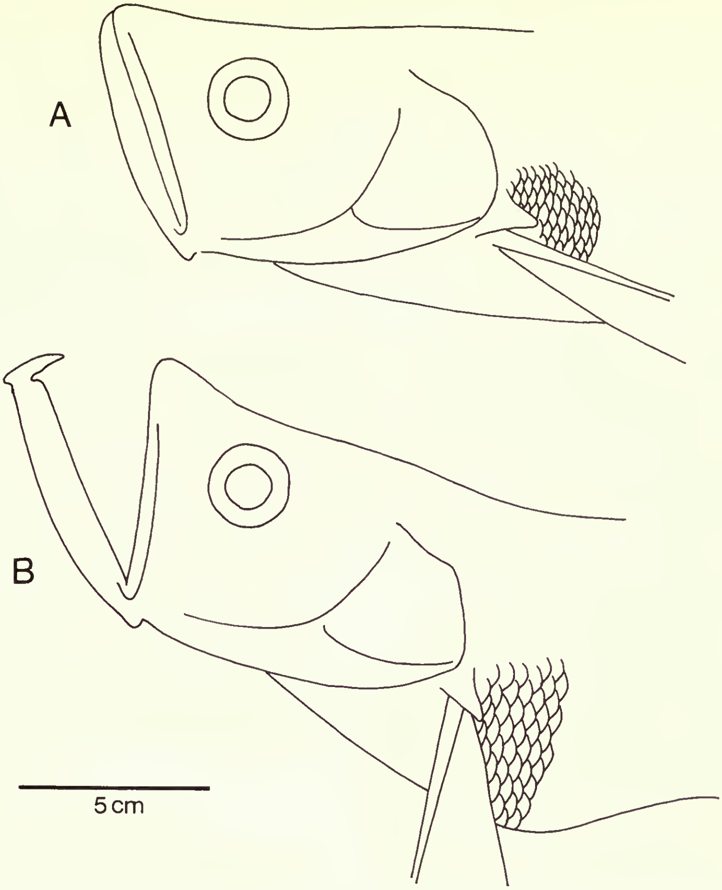

Fig. 37 *Macrochirichthys macrochirus*. Outline drawings of head, pectoral fin and associated scales in A. normal position, B. with head elevated. Note forward rotation of first pectoral fin ray, expansion of scale rows and ventral curvature of the abdomen. Drawings made from preserved specimens.

intraspecifically and is dependent upon the depth of the body, the degree of lateral compression and the condition of preservation of the specimens. It is, therefore, a character of limited value for defining genera.

A prominent axillary scale is situated behind the pectoral fin in both *Salmostoma* and *Securicula*; in *Securicula* it is developed as an elongate structure and is thickened along its lower border (Fig. 38). I have not found a scale of this type in any other cultrine genus, although in some a small, fleshy axial lobe may be present. Elongate axial scales are, however, present in some species of *Chelaethiops* and *Barilius* where they appear to be correlated with the extension of the pectoral fins. However, this correlation is not always evident as for example in *Leptocypris* where the pectoral fins are relatively short but the axial scale is between 50 and 75% their length. If the development of the scale is related to the size of the pectoral fin then one would have expected such a structure to be not only present but well-developed in *Macrochirichthys*. It may well be that in those taxa where it occurs it has a hydrodynamic function, perhaps as a fairing to reduce turbulence. Whatever function it may have, the axial scale is considered to be a derived character.

Discussion

From the observations presented here and from a previous description (Howes, 1976) several comments can now be made concerning the anatomy and phylogenetic relationships of *Macrochirichthys*.

Functional morphology

Earlier (Howes, 1976) I noted that certain features of the vertebral column of *Macrochirichthys* were indicative of some elevation of the skull. Confirmation of this type of mobility comes from observations made on aquarium specimens (pers. obs. and information provided by K. Purbrick and D. Bird) and freshly caught specimens (information provided by Dr T. R. Roberts).

The elevation of the cranium would seem to depend on two coordinated systems; (1) the movements of the upper section of the *epaxialis* muscle and its associated tendons, and (2) the rotation of the pectoral girdle.

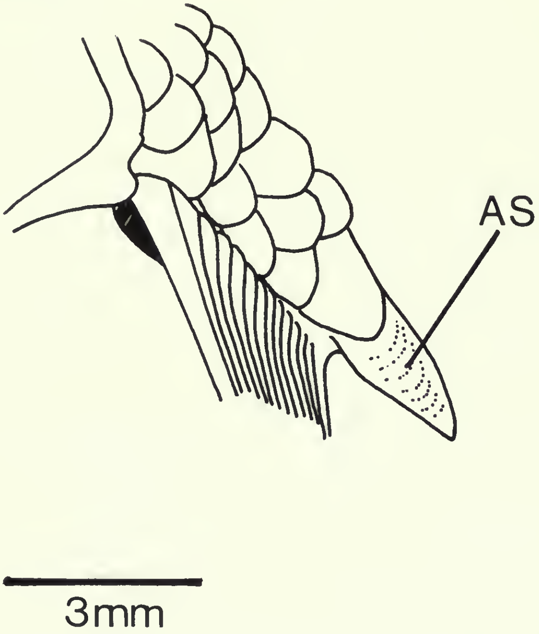

Fig. 38 *Securicula gora*, pectoral axial scale (pectoral fin has been moved downwards).

Presumably the principal force involved in raising the cranium is provided by the long tendinous fibres of the upper section of the *epaxialis* and the medial bands of tendon. The forces directed toward the midline and resulting in the elevation of the cranium are partially resisted by the interlocking system of neural arches and supraneurals (see p. 165) which preserve the shape and rigidity of the dorsal profile. The absence of true myosepta in the dorsal section of the *epaxialis* and the low angles of inclination of the fibres to the medial vertical plane demand the fibres shortening over long distances. The lateral beams provided by the cranial intermuscular bones would appear to form a rigid framework for this rather elastic movement. The lower part of the *epaxialis* which is attached laterally to the intermuscular bone beam, is arranged in helical layers (see p. 161). This arrangement of the muscle presumably aids in providing the necessary degree of lateral body bending.

The application of the term 'beam' to the unit of intermuscular bones although employed above in a descriptive sense can also have a functional usage. As Alexander (1968) has explained, if a beam is long and thin, tensile and compressive stresses acting on it will be high and if the beam is too slender it will fail by sideways bending. In *Macrochirichthys* the individual components of the beam, which can be thought of as elastic-like rods, allow the unit a great flexibility in the vertical plane (Fig. 39B). Each rod (bone) forms an arc when the skull is bent upwards (see Figs 39A & B) and its flexibility provides a restorative force to straighten the cranium. Likewise the flexible nature of the 'beam' allows twisting and bending in the horizontal plane. The tapering and thickening of the beam at its proximal end coincides with the point at which bending moments are greatest (see Alexander, 1968, 1969). The fact too that each bone of the

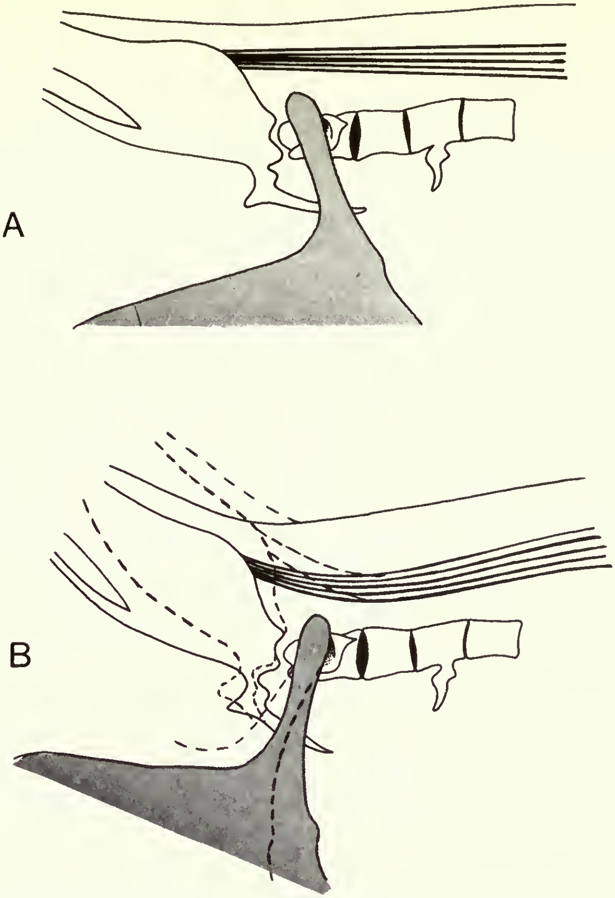

Fig. 39 *Macrochirichthys macrochirus*. Diagrammatic drawings of cranium, vertebral column and pectoral girdle showing association of the various elements when the cranium is elevated. A. Normal position. B. Elevated position of a manipulated preserved specimen, the dashed outline indicates the presumed position of the cranium and pectoral girdle in a living fish. Note: pivoting of pectoral girdle against lateral process of 2nd vertebra; bending of the cranial intermuscular bone beam and the enlarged 2nd–3rd intervertebral disc (black). Drawings made from radiographs.

beam is longer than the one above it suggests the equal proportioning of tensile and compressive stresses. The widely spaced and obliquely orientated bands of fibres of the lateral *epaxialis* allows the intermuscular bones to move relative to each other.

The downward movement of the pectoral fins would tend to rotate the pectoral girdle, thereby reinforcing the dorsal movement of the cranium effected through the system outlined above.

It was noted (p. 177) that the upper part of the cleithrum is only narrowly separated from, and attached by ligamentous tissue to, the transverse process of the 2nd vertebra. When the pectoral girdle is rotated the tip of the cleithrum pushes back against this process, which thus acts as a pivot (Figs 39 & 40).

Small aquarium specimens of *Macrochirichthys* are capable of rapid upward jerks of the cranium which at times make the head appear to lie almost at right angles to the horizontal axis of the body. The specimens in question were kept alive for less than 24 hours and were not fed, the head movements appeared to be a response to disturbance of their container. In preserved material, the cranium when maximally elevated, lies at an angle of 30–35° to the vertebral column.

The morphology of the cranial–vertebral joint in *Securicula* and *Chela* suggests that these species too are capable of a similar degree of head movement. Confirmation that this does indeed occur in *Chela* comes from the observations of Dr C. C. Lindsey. Lindsey (in press) found that *Chela maassi* could snap its head back almost at right angles to the contour of the back, that the elongate pectoral fins moved downward and that the fish was thus thrust upward. This 'neck-bending' and pectoral fin movement was used by the fishes when alarmed; if they were close to the water surface when the neck-bending occurred they would break through. Lindsey also noted that *Chela* skittered over the water surface, probably by utilizing rapid sequences of neck-bending.

Possibly this action, as well as allowing predator-avoidance, might also be used for catching prey at, or even above, the surface. As mentioned earlier (p. 173) the mouth of *Chela* is almost circular and if the head was almost vertical when it hit the water surface the mouth would act like a funnel.

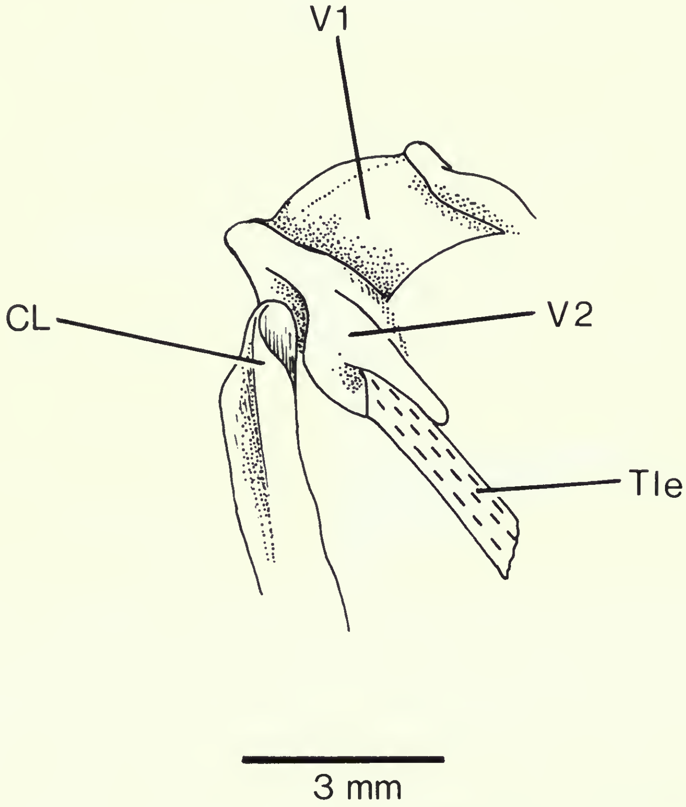

Fig. 40 *Macrochirichthys macrochirus*, pivot between cleithrum and 2nd vertebra.

Whether or not *Macrochirichthys* can elevate its head to the same degree as can some species of *Chela*, the head shape, orientation and length of jaws, and the elongation of the body suggest a rather different feeding action, one akin, in fact, to that of the characoids *Rhaphiodon* and *Hydrolycus* (see below).

In an earlier paper (Howes, 1976) I compared *Macrochirichthys* with the cynodontid characoid *Rhaphiodon* using these genera as an example of parallel evolution. Although almost exactly alike in external morphology, there are many differences in skeletal and muscle anatomy.

The crania of the two genera are alike in the angle at which the neurocranium is orientated to the vertebral column, and in the close union of the orbitosphenoid and the parasphenoid. However, in the characoid a large area of the cranial roof (the frontal and sphenotic) is utilized for the attachment of the *dilatator operculi* muscle, whereas in the cyprinid the cranium is largely covered by the extensive epaxial musculature, the *dilatator operculi* being small and originating only from the sphenotic.

Lesiuk & Lindsey (1978) have shown that *Rhaphiodon* is capable of a high degree of elevation of the cranium. The mechanism of this elevation differs from that of *Macrochirichthys* in that the articulation of the head with the vertebral column is *behind* the Weberian apparatus. This has necessitated a modification to the anterior part of the swimbladder (see Lesiuk & Lindsey, 1978). As explained above (p. 162) in *Macrochirichthys* articulation of the cranium with the vertebral column is between the basioccipital and the 1st vertebra and thus there is no modification of the swimbladder.

One further convergence between the two genera is the development in *Macrochirichthys* of long cranial intermuscular bone bundles and in *Rhaphiodon* of a cable-like tendon (see Lesiuk & Lindsey, 1978). No doubt these elements perform a similar function in both genera (see p. 182). It seems likely that the tendon in *Rhaphiodon* is the prime force in raising the cranium whereas the intermuscular bones in *Macrochirichthys* have a more complex function (see p. 182).

The precise method of prey capture by *Macrochirichthys* must await detailed analysis of such action in live specimens. It seems likely that the fish makes rapid darting movements towards its prey from an almost stationary position. Approach is possibly from below, *Macrochirichthys* arresting its speed by extending the pectoral fins laterally and forward and seizing the prey by a rapid backward jerk of the head. Some evidence for this method of capture comes from personal observations, and from first-hand accounts of the feeding behaviour of *Hydrolycus*, a characoid closely related to *Rhaphiodon* (see above). *Hydrolycus* makes rapid spurts forward and slashes at its prey, which it sometimes 'throws' or tosses before swallowing it.

Relationships of *Macrochirichthys*

Nomenclatural note

In the following analysis the name *Parachela* is used. The genus is defined on p. 189, but its introduction at this point is necessary to facilitate the discussion of relationships. *Parachela* includes all those species presently assigned to the genus *Oxygaster*, with the exception of *O. anomalura* which now remains the sole representative of the genus *Oxygaster*.

Macrochirichthys belongs to a group of genera characterized by the possession of the following synapomorphies:

1. A short supraethmoid overlapped by the frontals (see p. 152).
2. Narrow, medially depressed frontals with anteriorly converging canals (p. 151).
3. Modified triangular kinethmoid, sometimes articulating directly with the premaxillaries (p. 152).
4. Socket locking premaxillaries (p. 172).
5. Parasphenoid contacting pterosphenoid (p. 156).
6. A modified 1st centrum (tapered and anteriorly rounded) and second centrum (p. 162).
7. Neural complex sloped backwards and sometimes articulating with the first supraneural (p. 165).
8. Anterior supraneurals modified and articulating with succeeding elements (p. 165).
9. Horizontally aligned cranial intermuscular bones (p. 158).
10. Coracoid with a deeply incised ventral border or a reduced cleithral-coracoid fenestra (p. 177).
11. Short upright cleithral limb (p. 177).
12. Narrow, elongate supracleithrum (p. 177).
13. Modified postcleithrum (p. 177).
14. Anterior cranial extension of epaxial musculature (p. 150).

Characters 1, 3, 6, 11 and 13 are possessed by all the taxa included in the group, i.e. *Macrochirichthys*, *Parachela*, *Oxygaster*, *Securicula*, *Salmostoma* and *Chela*. This assemblage is hereafter referred to as the *cheline* group (see p. 187).

Characters 1 and 3 are also found in *Rasbora*, *Rasborinus*, *Aspidoparia* and *Danio;* characters 2 (part), 10, 11 and 14 are present in *Pelecus*. These genera are discussed on pages 191–194.

Chela can be immediately separated from the other cheline group genera on the basis of its cranial, pectoral girdle and axial skeletal morphology. The head is broad (wide frontals and supraorbitals); the mesethmoid protrudes far laterally on either side of the reduced supraethmoid and extends forward as a shelf (p. 154 & Fig. 8); the preethmoids are minute (p. 154); the kinethmoid is a small triangular lamellar bone (see Fig. 5D); the parasphenoid and orbitosphenoid are connected *via* a deep orbitosphenoidal septum; the dentary is extremely shallow; the enlarged supracleithrum almost covers the upright limb of the cleithrum (Fig. 36E); the fenestra between the coracoid and cleithrum is reduced or absent; the transverse processes on the 1st vertebra are enlarged and caudally directed; the supraneurals are enlarged, lamellar and interlock.

The modifications of the ethmoid region; the shape of the mouth (p. 173), and the deep body are adaptations associated with a trend toward specialized surface or aerial feeding habits (p. 184). These several autapomorphies characterize *Chela* as representing the sister group of the other genera included in the cheline assemblage (see cladogram, Fig. 41).

Salmostoma (with *Securicula;* see below) appears to represent the plesiomorph lineage of the cheline group. It displays what might be regarded as 'first-stage' modifications resulting in the apomorph character complexes present in its sister taxa.

The frontals barely overlap the supraethmoid; the kinethmoid is rod-shaped; the infraorbitals are expanded and the 5th contacts the supraorbital; the orbitosphenoid contacts the parasphenoid through a deep and narrow septum; the coracoids, although meeting each other along the midline, are not greatly expanded; the neural complex is long with an inclined dorsal border but is separated from the fourth neural spine; a quadrate-metapterygoid fenestra is present; the anal fin is short (14–20 rays).

Derived features in *Salmostoma* are the deeply notched ethmovomerine block; wide lateral commissure; trigemino-facialis foramen situated within the prootic face; laterally extended parietals; narrow elongate supracleithrum; reduced postcleithrum; acutely angled jaw with well-developed symphysial process (in some species; see p. 190).

Securicula, whilst retaining certain plesiomorph features (i.e. metapterygoid-quadrate fenestra; large 5th infraorbital contacting the supraorbital; short anal fin), possesses all the apomorph characters listed on p. 185, with the exceptions of 4 and 7. Although sharing with *Macrochirichthys*, *Parachela* and *Oxygaster* the incised coracoids, with *Macrochirichthys* and *Parachela* the medially depressed frontals and extended epaxial musculature, and with *Macrochirichthys* the contact between pterosphenoid and parasphenoid an even closer relationship with *Salmostoma* is suggested by the following synapomorphies: anterior trigemino-facialis foramen within the prootic (p. 156); narrow, elongate supracleithrum (p. 179); lateral processes of second centrum posteriorly directed, reduction of postcleithrum; elongate axillary scale. On the basis of these characters I consider *Securicula* to represent the sister group of *Salmostoma.*

Oxygaster possesses 1, 3, 6, 7, 10, 11 and 13 of the apomorph characters listed on p. 185. It shares only with *Parachela* and *Macrochirichthys* the kinethmoid articulating with the premaxillaries, the elongate curved postcleithrum, and the long anal fin (26–36 rays; see below).

Plesiomorph features of *Oxygaster* are the flat cranial roof with the frontal sensory canals confined to the lateral edge of the bones; well-developed dilatator fossa; lamellar supraneurals; a straight lateral line; large scales.

Oxygaster is here recognized as a monotypic genus (see p. 187) which, together with *Macrochirichthys* and *Parachela*, forms a sub-lineage of the cheline assemblage (see p. 187).

Parachela possesses all the apomorph characters listed on p. 185 apart from 5, 9 and 12. It shares only with *Macrochirichthys* the converging frontal canals, socket locking premaxillaries and elongate anterior supraneurals. Despite these synapomorphies there is still a large morphological 'gap' between the two genera. Like *Chela*, *Parachela* shows a trend towards a specialized deep-bodied habitus in which the lateral line is strongly decurved and follows the ventral border of the body.

From what has been said above *Macrochirichthys* is seen to belong to a subgroup of the cheline assemblage which also includes *Oxygaster* and *Parachela. Macrochirichthys* has tended towards an elongation of the body and, a correlated elongation of the anal fin, a character shared with the other two genera included in its subgroup (24–26 anal rays in *Macrochirichthys;* cf. 26–30 in *Oxygaster* and 26–36 in *Parachela*). Although *Macrochirichthys* is more highly derived than *Parachela* in terms of the specialized nature of the vertebral column and associated musculature, it still retains the overall plesiomorphic facies of the cheline group. Although *Parachela* lacks the high degree of vertebral modifications of *Macrochirichthys*, or even *Chela*, the morphology of the 1st and 2nd centrum and the anteriorly extended epaxial musculature suggest that it too is capable of elevating the cranium to a marked degree.

Thus, to summarize the interrelationships of the cheline group, it appears that the salmostomine lineage (i.e. *Salmostoma* and *Securicula*) form the sister group to the oxygastrine lineage (i.e. *Macrochirichthys*, *Parachela* and *Oxygaster*). Within this assemblage *Macrochirichthys* and *Parachela* share a common ancestor and form the sister taxon to *Oxygaster*. The salmostomine and oxygastrine lineages together comprise the sister group of the cheline lineage (i.e. *Chela*); see cladogram, Fig. 41.

Macrochirichthys, *Parachela* and *Oxygaster* have an almost completely overlapping distribution throughout the south-east Asian Archipelago, although, *Oxygaster* has not been recorded from Thailand or the Mekong drainage. *Salmostoma* is confined to India and Burma and its closest relative, *Securicula*, to eastern and northern India. *Chela* is widespread throughout India and the south-east Asian Archipelago.

One explanation of this distribution would be to suppose that the ancestral group which gave rise to the lineages now represented by the cheline group was present in India (or proto-India). If it be accepted that *Salmostoma* represents the plesiomorph lineage of this group, then it is likely that the basal dichotomy between the salmostomine and cheline lineages occurred in that subcontinent with subsequent establishment of the cheline (i.e. *Chela*) lineage in south-eastern Asia. *Securicula* is seen as evolving from the salmostomine lineage within India. The oxygastrine assemblage, however, appears to have developed only within the south-east Asian Archipelago.

The cheline group: taxonomy and interrelationships

Fowler (1905) first introduced the name 'Chelinae' under which he listed only *Macrochirichthys.* No definition of the Chelinae or indication of their status was given, but the use of the stem 'Chela' in this name implied the inclusion of the genus *Chela* with *Macrochirichthys.* Subsequently, Fowler (1934) placed both genera in the Abramidae, thus following the classification of Weber & de Beaufort (1916), a practice adhered to by all subsequent authors.

I have used the name cheline as an informal category and have purposely avoided its use as a subfamilial term because the interrelationships of this group with other taxa is at present imperfectly known (see Howes, 1978).

The most recent author to consider the taxonomy of the genera now assigned to the cheline group is Bănărescu (1967, 1968*a*, 1968*c*, 1969, 1971*a*). Most of these taxa he placed in the Cultrinae (Bănărescu, 1967). Despite Bănărescu's work there remain many problems concerning the taxonomy of the species now placed in the cheline group, and these are considered below:

Macrochirichthys Bleeker, 1860
Type: *Leuciscus uranoscopus* Bleeker, 1850
(=*Leuciscus macrochirus* Valenciennes, 1844)

Fowler (1905) described a second species of *Macrochirichthys* from Borneo, *M. snyderi.* This description was based on a single specimen which differed from specimens of *M. macrochirus* in possessing dark transverse bands across the nape. Later, Weber & de Beaufort (1916) placed *M. snyderi* in the synonomy of *M. macrochirus.* Fowler (1934) contested this decision, not only maintaining the validity of his species but describing yet another, *M. laosensis* from the Mekong River. Smith (1945), correctly in my opinion, relegated both *M. synderi* and *M. laosensis* to the synonomy of *M. macrochirus.*

Oxygaster van Hasselt, 1823
Type: *Oxygaster anomalura* van Hasselt, 1823

From the foregoing analysis it will be evident that there are major differences between the type

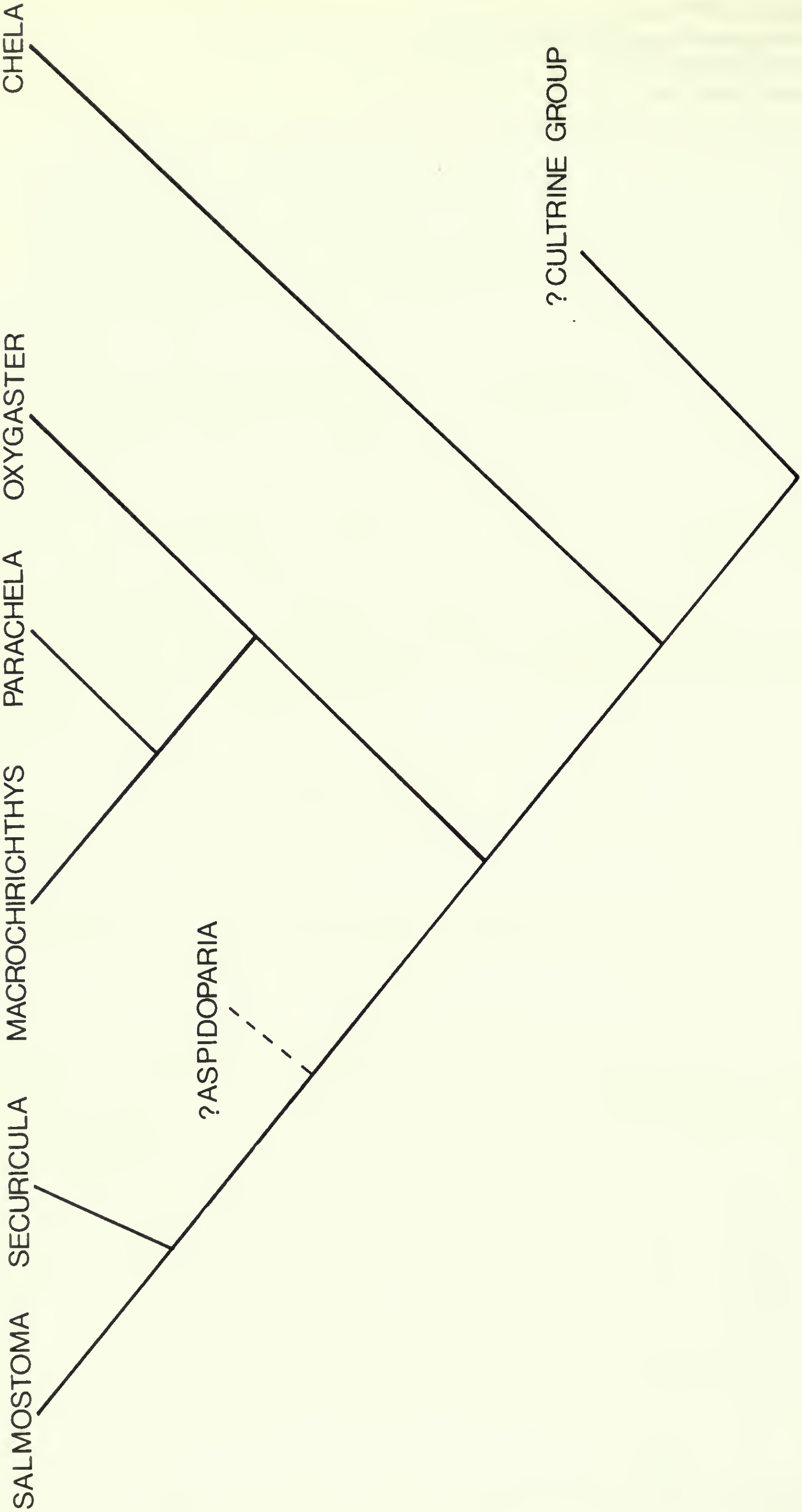
SALMOSTOMA
SECURICULA
?ASPIDOPARIA
MACROCHIRICHTHYS
PARACHELA
OXYGASTER
CHELA
?CULTRINE GROUP

Fig. 41 Cladogram illustrating phyletic relationships of the cheline group.

species of the genus *O. anomalura* and the other species presently assigned to the taxon (see Bănărescu, 1969). The differences between the species are listed below:

Oxygaster anomalura	Other *Oxygaster* species
Epaxial musculature extends to parietal	Epaxial musculature extends to anterior of frontals
Frontals flat or convex, sensory canals confined to lateral edges	Frontals depressed medially, canals converging anteriorly
Well-developed transverse parietal ridge	Parietal ridge absent
Long lower jaw with symphysial process	Short lower jaw with reduced symphysial process
Lateral process of 4th vertebra curved posteriorly	Lateral process of 4th vertebra curved anteriorly
Angle of neural complex to vertebral column 35°	Angle of neural complex 40–45°
Anterior supraneurals lamellar	Anterior supraneurals rod-shaped
Kinethmoid expanded dorsally	Kinethmoid curved anteriorly
Coracoids barely indented	Coracoids deeply incised
Supracleithrum elongate	Supracleithrum short

These morphological differences show that apart from cheline synapomorphies, *Oxygaster anomalura* possesses no other (derived) characters of the other *Oxygaster* species. I therefore consider that these other species be assigned to the genus *Parachela* (see below).

Parachela Steindachner, 1881
Type: *Parachela breitensteini* Steindachner, 1881
(=*Chela hypophthalmus* Bleeker, 1860)

This genus was characterized by Steindachner by its lacking of ventral fins. However, the description was based on a single, aberrant specimen (see below). Apart from this abnormality *Parachela brietensteini* possesses all the characters listed above under the heading 'Other *Oxygaster* species'. In accordance with those characters the species assigned to *Parachela* are:

P. oxygastroides (Bleeker, 1852)
P. hypophthalmus (Bleeker, 1860)
P. pointoni (Fowler, 1934)
P. williaminae Fowler, 1934
P. maculicauda (Smith, 1934)

Through the courtesy of Dr P. Kähsbauer I have been able to examine the holotype and unique specimen of *Parachela breitensteini*. There is no trace of ventral fins nor any part of the pelvic girdle (ascertained by radiography). Although abnormal in this respect, all other morphological and meristic characters show that *P. breitensteini* is a specimen of *Parachela hypophthalmus* (Bleeker, 1830) and should thus be included in the synonymy of that species.

Fowler (1934) described a second *Parachela* species, *P. williaminae* which he placed in a subgenus, *Grandisquamachela*, distinguished from *Parachela* by its larger scales (35 in the lateral line, cf. 60 in *P. breitensteini*. Bănărescu (1971*a*) found that Fowler's (1934) description was also based on an aberrant specimen and placed the species in the genus *Oxygaster*. I have not seen the type of *P. williaminae* and so am provisionally accepting Bănărescu's (1971*a*) contention that it is a valid species and is related to *P. oxygastroides*.

The species here assigned to *Parachela* were revised by Bănărescu (1969) and for the most part I agree with his synonymies. However, concerning the taxon *pointoni*, Bănărescu (1969) recognized *Chela pointoni* Fowler, 1934 as a valid species (of *Oxygaster*, i.e. *Parachela*) but later (Bănărescu, 1971*a*) he considered it to be a subspecies of *Oxygaster anomalura* van Hasselt, 1823. I have not seen the holotype of this species but from Fowler's description and the photograph published by

Bănărescu (1969) it is clear that the epaxial muscles extend forward to the interorbital area and therefore the taxon should be referred to the genus *Parachela*. Its specific status must remain in doubt; according to Bănărescu (1969) there are '. . . some 36 scales' in the lateral line, yet later (1971*a*) he gives a count of 43–44; Fowler (1934) in his original description gives 33. If Bănărescu's 1971*a* description is correct then I see no reason why *P. pointoni* should not be included in the synonymy of *P. oxygastroides*. Taki (1974) records *P. pointoni* from Laos, but his photograph is of an *Oxygaster* species, close to, or identical with *O. anomalura*.

Salmostoma Swainson, 1839

Type: *Cyprinus bacaila* Hamilton-Buchanan, 1822

This genus belongs to the plesiomorph sister-group of the oxygastrine lineage (see p. 187). The most recent revision is by Bănărescu (1968*a*) who recognizes 10 species. I have the following comments concerning these species.

Salmostoma bacaila (Hamilton-Buchanan, 1822). The development of the symplectic and the associated metapterygoid-quadrate fenestra in this species have been commented on earlier (p. 175). It was considered that the nature of this feature, together with the long jaws, are indicative of a relatively derived status. This is further indicated by the elongate, deeply notched ethmoid region and the well-developed symphysial hook on the lower jaw. Bănărescu (1968*a*) states that this species is '. . . the most frequent of all', but then notes that its range is restricted to the Indus and Ganges drainages.

Salmostoma clupeoides (Bloch, 1782). As Bănărescu (1968*a*) suggests, this species may simply be a subspecies or perhaps a clinal group of *S. bacaila* from which it appears to differ only in the number of lateral line scales.

Salmostoma phulo (Hamilton-Buchanan, 1822). I cannot agree with Bănărescu's (1968*a*) division of this species into two subspecies, separated by a difference in the number of lateral line scales (99–112 in *phulo phulo* cf. 76–86 in *phulo orissaensis*). Later, Bănărescu (1971*a*) recorded the subspecies *orissaensis* from Madras based on a single specimen with a lateral line count of 89, thus extending the range of this 'subspecies' for a further 700 miles. I have examined the types of *S. phulo orissaensis* and find many differences, apart from lateral line scale counts, between them and specimens of *S. phulo phulo* (e.g. shape of the 5th infraorbital; interorbital width; pectoral fin length; lower jaw length; shape of axillary scale), all of which Bănărescu has ignored but which I believe indicate specific rather than subspecific status.

Salmostoma punjabensis (Day, 1872). Bănărescu (1968*a*) suggests that this taxon is possibly a subspecies of *S. phulo*. This is highly unlikely as *S. punjabensis* is known only from the Indus and *S. phulo* only from Assam, a separation of some 28° of latitude. My own comparison of the two types suggest these are indeed two quite distinct species characterized by differences in snout, jaw and pectoral fin length. Bănărescu (1968*a*) does not give measurements of the pectoral fin length which appears to be an important character in separating species of this genus.

Salmostoma horai (Silas, 1951). Bănărescu (1968*a*) did not examine any specimens but accepted this as a valid species on the basis of Silas' description. Silas (1951) remarks that the lower jaw has a well-developed symphysial process and that the species differs from its congeners in possessing short vertical bands along the flanks.

Salmostoma acinaces (Valenciennes, 1842). A large scaled species which will probably prove to be polyspecific.

Salmostoma untrahi (Day, 1869). Bănărescu (1968*a*) noted the vertically aligned mouth and the long symphysial process of the lower jaw, this process is not developed in a specimen of 65 mm SL. Elsewhere I have commented on these features (p. 186) and suggest that *S. untrahi* represents, like *S. bacaila*, a specialization towards the morphotype of *Securicula*.

Salmostoma boopis (Day, 1869). Bănărescu (1968*a*) notes. 'This species is close to *S. acinaces*, differing from it in number of scales, rays and gill rakers (but with overlap of extreme values!)'. I find that there is an overlap in all meristics and it seems likely that *S. boopis* is a synonym of *S. acinaces* (part).

Salmostoma sardinella (Valenciennes, 1842). Comments have already been made concerning the form of the metapterygoid-quadrate fenestra in this species (p. 175) and its relatively specialized nature.

Salmostoma sladdoni (Day, 1869); the only species of the genus apparently restricted to Burma.

Bănărescu (1968*a*) groups the species of *Salmostoma* into four lineages on the basis of geographical distribution. Such a grouping is impossible on the material currently available, the total collections of which amount to *c.* 150 specimens (based on Bănărescu, 1968*a*). This interesting genus must be critically revised on an osteological basis before any assumptions can be made concerning intra-generic relationships.

Securicula Günther, 1868

Synonymy: *Pseudoxygaster* Bănărescu, 1967
Type: *Cyprinus gora* Hamilton-Buchanan, 1822

Bănărescu (1967) erected the genus *Pseudoxygaster* for the species *gora* which previously had been assigned by various authors to either *Chela* or *Oxygaster*. Günther (1868) had divided the genus *Chela* into two sections on the grounds of differences in the pectoral girdles. One of these divisions he named *Securicula* and included *gora* as the first-named species. Jordan (1919) recognized *gora* as the type species of *Securicula* by logotypy. Bănărescu (1967, 1968*a*) treated *Securicula* as a synonym of *Salmostoma*, presumably on the assumption that the other species listed by Günther under *Securicula* are now recognized as belonging to the genus *Salmostoma*. I can find no grounds for not recognizing *Securicula* as a distinct taxon and accordingly treat *Pseudoxygaster* as its junior synonym.

The genus is monotypic, although Bănărescu (1967) considered the possibility that there are two subspecies, an opinion based on a single specimen having fewer lateral line scales than the type.

Bănărescu (1967) thought *Securicula* to be closely related to *Macrochirichthys* and *Pelecus*. Mirza, Alam & Kausar (1974) and Mirza (1975) noted the presence of the metapterygoid-quadrate fenestra and Mirza (1975) considered the genus to be 'the most primitive of the Cultrinae of south Asia'. Contrary to this opinion I believe *Securicula* is the most highly evolved member of the Salmostomine lineage (see p. 187).

Chela Hamilton-Buchanan, 1822

Type: *Chela cachius* Hamilton-Buchanan, 1822

The most complete revision of the genus is that of Silas (1958) who recognized the subgenera *Allochela* and *Neochela* on the basis respectively of a complete or incomplete lateral line. Bănărescu later (1968*c*) recognized a third subgenus *Malayochela* with the pharyngeal teeth arranged in two instead of three rows as in the other taxa. However, Bănărescu states that this is a variable character in other cyprinid genera – which it is – and therefore I see little to justify the subgenus *Malayochela*. There are, on the other hand, distinct differences in the development of the transverse processes of the 1st and 2nd vertebrae. Whether these differences are species specific or whether they can be used to define groups of species remains to be verified.

The relationships of *Chela* have been discussed on p. 186; the genus is seen as representing a highly evolved group of surface or aerial feeding specialists which departed early from the basic cheline stock.

Of the characters listed on p. 185 defining the cheline group, one – the frontals overlying the supraethmoid – is shared with *Aspidoparia*, *Rasbora*, *Rasborinus* and *Danio*; furthermore, a second feature – the expanded kinethmoid – is found in all but *Aspidoparia*. These four genera pose acute problems in determining phylogenetic relationships and will be discussed in greater detail.

Aspidoparia Heckel, 1843

Type: *Aspidoparia sardina* Heckel, 1843
(= *Cyprinus morar* Hamilton-Buchanan, 1822)

This genus shares with the other taxa assigned to the cheline group a short, triangular supraethmoid; anteriorly the ethmo-vomer block is deeply notched and posteriorly the supraethmoid is covered by the frontals. However, the entire ethmoid block is short and strongly decurved anteriorly. *Aspidoparia* also shares with other chelines an elongate first supraneural which articulates with the neural complex. As in *Salmostoma* the kinethmoid is rod-shaped, the infraorbitals large (the 5th contacting the supraorbital), the orbitosphenoid is joined to the parasphenoid by a deep septum and there is a metapterygoid-quadrate fenestra (the smallest aperture of this nature in any of the genera possessing it – see p. 177). All these characters shared with *Salmostoma* are plesiomorph for the cheline group, as are the gently curved lateral line and short anal fin (9–12 rays).

Aspidoparia differs from other genera assigned to the chelines in the following features; the 1st vertebra is neither anteriorly tapered nor rounded and it bears strong, somewhat anteriorly directed lateral processes; the neural complex is upright and not inclined backwards; the cleithrum is upright and has a high anterior ridge along its horizontal arm (resembling the condition in *Danio*); and finally the reduced parietals and well-developed supraoccipital process.

The jaws of *Aspidoparia* are markedly different from any cheline or for that matter, any cultrine. They are short, the lower jaw being curved strongly medially and the entire mouth inferiorly placed. The coronoid process of the obliquely angled dentary is situated at the middle of that bone. From the roof of the mouth there hangs a thick papillose nodule originating from below the vomer. The intestine of *Aspidoparia* is much coiled (the specimens dissected contained fine mud and silt in the gut).

Sorescu (1968) placed *Aspidoparia* amongst the cultrines because of resemblances between its pectoral girdle and those of certain other genera. By my definition of the cultrine group *Aspidoparia* cannot be placed there (p. 197). The synapomorphies mentioned above may be indicative, however, of a shared common ancestry between *Aspidoparia* and *Salmostoma*, in which case *Aspidoparia* can be seen as representing a specialized detrivorous branch of the cheline group (see Fig. 41).

There appear to be two species of *Aspidoparia*; *A. morar* (Hamilton-Buchanan, 1822) and *A. jaya* (Hamilton-Buchanan, 1822). The species *siamensis* Sauvage, 1881, originally placed in the genus *Morara*, was placed in *Aspidoparia* by Smith (1945). He quoted Pellegrin as saying that *siamensis* did not belong to *Aspidoparia*, but although Smith included it in that genus he did so with hesitation. I have not seen Sauvage's specimens of *Morara siamensis* and so the correct placement of this taxon must await a revision of this species group.

As mentioned above (p. 191) three other genera also share some of the characters used in defining the cheline group. These are *Rasbora*, *Rasborinus* and *Danio*.

The ethmoid region of some *Rasbora* species (including the type of the genus, *R. rasbora*) closely resembles that of *Chela* in that the mesethmoid extends laterally beyond the borders of the supraethmoid and protrudes as a shelf; the kinethmoid is also of the same lamellar type. Not all species of *Rasbora* possess these characters and some species (i.e. *R. argyrotaenia* and *R. dusonensis*) share derived characters with *Luciosoma*.

In *Rasborinus* and some species of *Danio* the ethmo-vomer is deeply notched anteriorly as in the chelines and cultrines (see p. 194).

As with *Rasbora* there is a similar problem concerning the genus *Danio*. The species I have examined appear to have marked differences in certain characters, particularly in the form of the lower jaw. In *Danio dangila*, the type of the genus, the antero-ventral part of the dentary bears a semicircular notch, there is a strong lateral flange on the coronoid process of the dentary, and the kinethmoid is of a type closer to that of *Rasbora* than to the other *Danio* species. In *Danio malabaricus*, *D. aequipinnatus* and *D. spinosus* the kinethmoid is of the lunate type illustrated in Fig. 5E; the notch on the ventral surface of the dentary is widely separated from its fellow along the midline, thus forming a characteristic arrow-shaped gap when viewed from below (Fig. 42), and there is a crenelated fleshy ridge along the margin of the lower jaw. *Danio devario* differs from all these species not only in the rhomboidal form of the body but in the morphology of the ethmoid region, which resembles that of *Chela*. It lacks, however, any of the characters used to define the cheline group, apart from the overlapping of the dermethmoid by the frontals and the triangular lamellar kinethmoid.

The composite genera *Danio* and *Rasbora* must be revised before any phylogenetic relationships can be established between their various included taxa. Thus, at present I cannot say if *Rasbora sensu stricto*, *Danio sensu stricto* and *Rasborinus* are more closely related to the cheline than to any other group; indeed I am not even sure that the three taxa are closely related to each other.

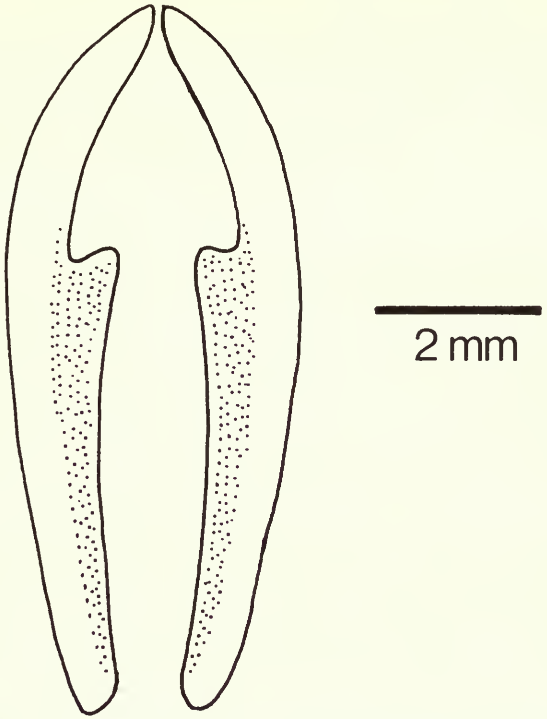

Fig. 42 *Danio malabaricus*, ventral aspect of the lower jaw.

Although *Rasbora sensu stricto*, *Danio sensu stricto* and *Rasborinus* share with the cheline group similarly modified ethmoids, there are no similar vertebral modifications. Whether such changes in the ethmoid region (i.e. overlap of the supraethmoid by the frontals) must necessarily be correlated with rearrangements in the structure of the vertebral column – as seems to have been the case in the chelines – is uncertain. However, studies on the African cyprinid genera *Engraulicypris* and *Chelaethiops* indicate that such changes in the ethmoid region are a 'prerequisite' to vertebral modifications.

Comments on the Cultrinae and relationships with the cheline group

The problem now remains as to the relationships of the cheline group with other assemblages of cyprinids and in this context the interrelationships of the taxa referred to the subfamily Cultrinae (to which the cheline genera are currently assigned) must be evaluated.

Of all the cyprinid subfamilial assemblages recognized at present there is probably none so ill-defined as the Cultrinae. Nikolsky (1954, 1955) first used the subfamily designation to include some genera which had previously been placed in the Abramidae, Xenocyprinidae and Danioninae. Silas (1958), in his review of *Chela*, pointed out that the Abramidinae (he made no mention of the Cultrinae; no doubt having overlooked Nikolsky's introduction of the taxon) seemed a group of convenience rather than a natural assemblage and thought that it included two major sub-groups, one in Thailand and the Malayan sub-region, the other in China.

Bănărescu (1967) reviewed the Cultrinae, outlined its taxonomic history and pointed out the difficulties in defining the taxon. The characters Bănărescu used were entirely superficial and apparently indiscriminate ones, and although he thought the subfamily represented a monophyletic unit he produced no arguments to show why. In fact his statement that the monophyly of the Cultrinae is 'less evident' than that of some other subfamilies, and again 'the relationships between these genera are obscure' indicates Bănărescu's uncertainty about the monophyletic integrity of the 21 genera he included in this group. Later, Bănărescu (1970*a*) makes the point that the 'delimitation of the genera within the Cultrinae is difficult and rather arbitrary, while the species are in general well-differentiated'.

Sorescu (1968) studied the pectoral girdle in various cyprinids. On the basis of this study she made radical taxonomic changes by placing *Aspidoparia morar*, *Barilius zambesensis* and *Alburnus alburnus* in the Cultrinae. However, as pointed out by Howes (1978), she misinterpreted various similarities as indicating relationship instead of parallelism, and made no attempt to support her conclusions by using other morphological characters.

During the course of studying *Macrochirichthys* I have had the opportunity to examine representatives of the genera placed in the Cultrinae by Bănărescu (1967) and by Sorescu (1968). The following comments may serve to clarify the taxonomy and interrelationships of these taxa.

Culter Basilewski, 1855
Type: *Culter alburnus* Basilewsky, 1855
Erythroculter Berg, 1909
Type: *Culter erythropterus* Basilewsky, 1855
Ischikauia Jordan & Snyder, 1900
Type: *Opsariichthys steenackeri* Sauvage, 1883

These closely related genera can be considered together. All three share an almost identical cranial anatomy, i.e. deeply notched ethmoid, an anteriorly projecting vomer, well-developed and ovate preethmoids, narrow skull, long post-parietal platform (formed from the supraoccipital, parietal and epioccipital – see Howes, 1978), truncated supraoccipital process, well-developed posttemporal fossae, large dilatator fossae, formed from the frontal and sphenotic, the sphenotic process produced latero-posteriorly, the orbitosphenoid and parasphenoid in close contact, extensive intercalar, wide ectopterygoid, a quadrate foramen, short upper and lower jaws with a high coronoid process on the dentary, and a wide, vertically aligned neural complex.

Many of these characters are widespread amongst cyprinids and must therefore be regarded as plesiomorph. However, there are indications that the morphology of the ethmoid region, of the post-parietal area of the cranium, and of the pectoral girdle, will provide useful characters positively to link these genera with others considered below.

Culter and *Erythroculter* differ from each other in the form of the lower jaw, which is also shorter in *Culter* (contained twice in head length, cf. 1·5 times in *Erythroculter*). The coronoid process is situated at the posterior end of the lower jaw in *Culter* whereas it lies midway along the jaw in *Erythroculter*. Other differences are to be found in the width of the supraorbitals and length of the nasals.

Ischikauia most closely resembles *Erythroculter* but differs both from that genus and from *Culter* in possessing a flexible 2nd dorsal spine instead of a well-ossified one.

Berg (1964 : 360) stated that *Erythroculter* is 'like *Culter* but abdomen keeled only behind the ventral base'. I doubt whether such a character by itself has any use in determining generic-level relationships (see p. 180).

Despite the fact that there have been two revisions of the genus *Erythroculter* (Yih & Chu, 1959 – not seen; Bănărescu, 1967) both this genus and *Culter* have been inadequately defined and much nomenclatural confusion still exists. Bănărescu (1967), following Yih & Chu (1959), states that *Culter erythropterus* Basilewsky, the type species of the genus *Erythroculter* is in fact synonymous with *Culter alburnus* and therefore *Erythroculter* must become a synonym of *Culter*. As pointed out above there are significant differences between *Culter* and *Erythroculter*. In the course of this study specimens of *Culter alburnus*, *Culter brevicauda*, *Erythroculter ilishaeformis* and *Erythroculter mongolicus* were examined. The type specimens of *Culter erythropterus* are apparently lost (Bănărescu, 1967) and if, as seems likely from the description of Basilewsky (1855), *erythropterus* is a synonym of *alburnus*, then *Erythroculter* must be a junior synonym of *Culter*. But, since there are synapomorph characters relating the species *ilishaeformis*, *dabryi*, *hypselo-*

notus, *oxycephaloides* and *mongolicus* which are not possessed by those referred to the genus *Culter*, the former group will have to be referred to the genus *Chanodichthys* Bleeker, 1860 (the next available name) with *mongolicus* as the type of the genus.

The nomenclatural problem concerning the type species of the genus *Culter* was satisfactorily resolved by Myers (1940). This genus is in need of a thorough revision and the generic status of some species (e.g. *C. tientsinensis* Abbott, 1901 and *C. kashinensis* Shaw, 1930) has to be clarified.

Longiculter Fowler, 1937
Type: *Longiculter siahi* Fowler, 1937

This is a perplexing taxon known only from the unique holotype. Fowler's (1937) statement that *Longiculter* differs from other cultrine genera in the elongate and compressed body means virtually nothing (see Smith, 1945). What is important is that the species appears to possess over 100 gill-rakers (rarely above 30 in cultrines and oxygastrines).

Bănărescu (1967, 1971*a*) accepts *Longiculter* as a valid genus. In his 1971*a* paper Bănărescu simply states 'Agree with Fowler's description', and he gives a gill-raker count of 107–128 (Fowler gives 106).

Both this genus and the *Culter* species recorded from Thailand need to be re-examined critically. Regrettably I have no specimens of these taxa to hand but I suspect that the '*Culter*' of Thailand will be found to be quite a different entity from the '*Culter*' of China. Hora (1923) pointed out the differences between *Culter siamensis* and the other species assigned to that genus (see also Smith, 1945 : 87 on this point). Whether these Thailand forms will have to be placed in the cultrine or cheline group must await the availability of further specimens.

Megalobrama Dybowski, 1872
Type: *Megalobrama skolkovii* Dybowski, 1872
(= *Megalobrama terminalis* (Richardson), 1846)

This genus has the same osteological characteristics as *Erythroculter*, but the member species are deeper bodied, have wider crania and less oblique mouths. One important character is the presence of sharp-edged horny sheaths in the upper and lower jaws.

The genus *Sinibrama* was established by Wu (1939) for the species *Megalobrama macrops* Günther. Wu (1939) distinguished *Sinibrama* from *Megalobrama* on the basis of its shorter anal fin and bipartite (cf. tripartite) swimbladder. Bănărescu (1970*a*) considered this division worthy of only subgeneric rank. However, there are differences in the structure of the mouth, the horny sheaths being absent in *M. macrops*, which also has a different pattern of fleshy folds in the buccal cavity. I have also found differences in the structure of gill-rakers between *macrops* and other *Megalobrama* species.

Parabramis Bleeker, 1864
Type: *Abramis pekinensis* Basilewski, 1855

This genus has the same osteological characters as *Erythroculter*. However, the infraorbitals are more reduced than in that genus, the pharyngeal teeth are pointed and the ventral keel extends forward of the ventral fins (although this character is of a somewhat dubious nature, see p. 180).

Ancherythroculter Wu, 1964
Type: *Chanodichthys kurematsui* Kimura, 1934

I have been unable to examine specimens of any of the species assigned to this genus. According to Bănărescu (1967) *Ancherythroculter* is separated from *Erythroculter* on the basis of a bipartite (cf. tripartite) swimbladder, differences in the length of the anal fin and the shape of the scales. Bănărescu (1971*a*) recognized these as 'good generic' characters but earlier (1970*a*) in the case of *Megalobrama* and *Sinibrama* had considered the same characters as worthy of only subgeneric distinction (see above).

Rasborinus Oshima, 1920
Type: *Rasborinus takakii* Oshima, 1920
(=*Rasborinus lineata* (Pellegrin), 1907)

Mention has already been made of the possible relationship between this genus and *Danio* (p. 192).

Paralaubuca Bleeker, 1863
Type: *Paralaubuca typus* Bleeker, 1863

The osteology of the cranium and the axial skeleton is typically that of *Culter*. The distinctive character of this genus lies in the two quite separate lateral lines on the anterior part of the body (in some specimens there may even be three; see Bănărescu 1971*b* : 348).

Pseudolaubuca Bleeker, 1864
Type: *Pseudolaubuca sinensis* Bleeker, 1864

The cranium is narrow and convex across the interorbital region. The orbitosphenoid and parasphenoid are widely separated by an orbitosphenoid septum. The ethmoid region, the first vertebra and neural complex are like those of *Culter*. There is an elaborate development of the supraneurals (see p. 170, Fig. 25) like that found in *Chela*. A parallel feature shared with *Macrochirichthys* is the lateral process of the hyomandibula. A revision of the genus was made by Bănărescu (1964).

Hemiculter Bleeker, 1859
Type: *Culter leucisculus* Basilewski, 1835

The cranium is as in *Pseudolaubuca*, but the premaxillary processes are elongate. This genus is almost identical with *Toxabramis* save for the possession of a non-serrated dorsal spine, a character which in other cyprinid genera (e.g. *Barbus*) is not indicative of generic status.

Bănărescu (1968*b*) revised the species of *Hemiculter* but made no mention of the relationships of the genus.

Toxabramis Günther, 1873
Type: *Toxabramis swinhonis* Günther, 1873

Toxabramis is distinguished from *Hemiculter* because its pharyngeal teeth are in two and not three rows and it has a serrated and not a flexible dorsal fin spine. I have been unable to examine the osteology of *Toxabramis* in detail but superficial dissection of one of the syntypes of *T. swinhonis*, and an examination of radiographs, reveals a *Culter*-type organization of the cranial and axial skeletons. A revision of the genus was made by Bănărescu (1963).

Hemiculterella Warpachowski, 1887
Type: *Hemiculterella sauvagei* Warpachowski, 1887

The cranium is wide and flat; the orbitosphenoids are closely joined with the parasphenoid; the infraorbitals are large and the supraorbital almost contacts the 5th infraorbital. The lateral line is deeply curved anteriorly and follows an erratic course. The dilatator fossa is small and roofed by the frontal. The second dorsal spine is well-ossified.

The relationships of *Hemiculterella* are discussed below, p. 197. Possibly not all species presently ascribed to this genus should be included in it (see Bănărescu, 1971*a*).

Pelecus Agassiz, 1835
Type: *Cyprinus cultratus* Linnaeus, 1758

The cranium is wide and flat posteriorly; the frontals are depressed medially and accommodate the anterior extension of the epaxial musculature; the infraorbitals are reduced and the supraorbital is small; the lower jaw is short and without a symphysial extension; the supraneurals are well-developed; the lateral line is deeply curved anteriorly and follows an erratic course; the lateral line scales are numerous (90–115).

Pelecus is the only supposedly European representative of the Cultrinae and was included in this subfamily by Bănărescu (1967) on the grounds of its close resemblance to *Oxygaster* and *Macrochirichthys*. However, it differs in many respects from those and other cheline genera. The cranium, although showing a development of the frontals similar to that in *Macrochirichthys*, *Parachela* and *Securicula*, is wide posteriorly and has reduced parietals; an extensive autosphenotic accommodates a large dilatator and posttemporal fossae cf. pages 152–153); the supraethmoid is posteriorly sutured to the frontals instead of being overlapped by them. Although *Pelecus* resembles the cheline genera in the alignment of the neural complex, there are marked differences in its basic morphology. The second neural plate is reduced; the neural complex is greatly expanded antero-posteriorly and contacts the first supraneural above the 5th centrum, cf. 7th or 8th in *Macrochirichthys*; the supraneurals are lamellar. The 1st vertebra, although having a well-rounded anterior face, possesses broad lateral processes, the ends of which are directed ventro-posteriorly. Other differences from members of the cheline group are evident in the pectoral girdle. The upright part of the cleithrum in *Pelecus* is broadly lamellar; the supracleithrum extends halfway along the cleithrum; the postcleithrum is short and straight; the posterior border of the coracoid is straight and although, as in *Parachela* and *Securicula*, the ventral coracoid border is incised, the nature of this indentation is quite different (see p. 180; cf. Figs 33B & 35C).

Although, as already mentioned, *Pelecus* possesses some of the apomorph characters listed on p. 185 as defining the cheline group, it lacks the characteristic morphology of the ethmo-vomerine region (p. 153). Furthermore, the vertebral column and pectoral girdle, although similar to those structures in the chelines are, in their basic morphology, more akin to those like structures in some leuciscines (see also Gosline, 1974 who includes *Pelecus* in the leuciscines). In short, they are the result of parallel evolution. Perhaps it is more correct to consider this as convergent evolution when it is remembered that *Pelecus* spends much of its life in brackish water where it appears to behave in a rather clupeoid fashion. Thus, those features in which it resembles some of the cheline genera may have been acquired under the different selection pressures of an esturine environment. This has resulted in the evolution of similar pelagic characters to the chelines but in dissimilar associations.

A likely candidate as the closest relative to *Pelecus* is *Hemiculterella*. With this genus *Pelecus* shares the flat, posterior cranium; the extensive sphenotic and dilatator fossa and the zig-zagged lateral line.

To recapitulate; of the twenty-one genera listed by Bănărescu (1967) as belonging to the Cultrinae, only six are thought to constitute a monophyletic assemblage – the cheline group. Of the taxa placed in the Cultrinae by Sorescu (1968) *Aspidoparia* has already been discussed (pp. 191); *Barilius zambesensis* although belonging to a discrete group of bariliines (unpublished obs.) possesses no derived characters which would include it amongst the cultrines; *Alburnus alburnus* may have a closer affinity with certain cultrines than do other taxa currently placed in the Leuciscinae. Of the remaining genera two related assemblages can be recognized.

I The *cultrine group*, comprising *Culter*, *Erythroculter*, *Ischikauia*, *Parabramis*, *Megalobrama* and *Paralaubuca*.

II The *hemicultrine group*, comprising *Hemiculter*, *Pseudolaubuca* and *Toxabramis* (possibly *Rasboriichthys* (part) should also be included here).

Two other genera included in the Cultrinae by Bănărescu (1967), *Pelecus* and *Hemiculterella*, are believed to be closely related to one another but not to any of the taxa listed above. Their relationships would seem to be with the Leuciscinae *sensu lato*.

Rasborinus appears to be related to *Danio* (see p. 192), a genus not included in the Cultrinae by Bănărescu (1967).

The affinities of *Ancherythroculter* are at present unknown (p. 195), but do not appear to be with the cultrine or hemicultrine groups.

In his discussion on the relationships of the Cultrinae, Bănărescu (1967) mentions the genus *Nematabramis* which Weber & de Beaufort (1916) placed in the Abramidinae (thus including it with *Chela* and *Macrochirichthys*). Bănărescu (1967) does not accept any relationship between *Nematabramis* and any of his cultrine genera but states that it is 'evidently related to the Danioinae especially to *Esomus*'. *Nematabramis* is a peculiar taxon; there are transverse ridges along the surface of the frontal (Howes, 1978), a highly modified ethmoid region, a membraneous maxillary barbel and other characters which do not immediately suggest a close relative. I can find no osteological evidence to suggest a close relationship between *Danio sensu stricto* and *Esomus* as is implied by Bănărescu (1967, 1971*b*).

The other group mentioned by Bănărescu (1967) as being a likely relative of the Cultrinae is the subfamily Xenocypridinae. According to Bănărescu (1970*b*) the characters defining this subfamily are: an inferior transverse mouth, smooth dorsal spine and compressed pharyngeal teeth with long grinding surfaces. I have examined the type species of *Xenocypris*, *X. argentea* and find that the dentary is extremely shallow and short, but it is broad so that medially it is narrowly separated from its fellow; the coronoid process of the lower jaw is high with a concave border; the ethmoid complex is deeply notched anteriorly and that there is an anterior chamber of the subtemporal fossa.

Two other genera are included in the Xenocypridinae, *Plagiognathops* and *Distoechodon* (sometimes recognized as subgenera of *Xenocypris*; see for example Nichols, 1943). Bănărescu (1970*b*) recognizes *Plagiognathus* as a valid, monotypic genus but *Distoechodon* as a 'polytypic subgenus'! From my own limited observations it appears that there is considerable difference in the structure of the gill-rakers between these various taxa. For example, *Plagiognathus microdon* more closely resembles *Xenocypris* (*Disteochodon*) *tumirostris* in this character than do either of these taxa resemble *Xenocypris argenteus*. As yet I have been unable to ascertain that they all share the apomorph osteological characters of *Xenocypris argenteus* listed above. This entire group is in need of critical revision and like so many other cyprinid 'subfamilies' the Xenocypridinae appears to be polyphyletic.

Mirza (1975) thought the Cultrinae to be most closely related to the *Danioinae* but in the light of the comments concerning the composite nature of the genus *Danio* (p. 192) the designation 'Danioinae' is meaningless. The basis Mirza chose for this relationship was the shared possession of the metapterygoid-quadrate fenestra in some members of the Cultrinae and in *Opsariichthys* and *Zacco* (presently included in the Danioinae). As pointed out elsewhere (p. 177; Howes, 1978) this character is plesiomorphic for the cyprinids and so cannot be regarded as an indicator of shared recent common ancestry. From work presently in progress it seems that *Opsariichthys* is not related to any member of the cheline or cultrine groups; indeed, its closest living relatives are currently included in the genus *Barilius*.

Thus, at present the identity of the sister-group to the chelines must remain in doubt. It seems that a likely candidate will be identified as a monophyletic assemblage of taxa included here within the cultrine and hemicultrine groups (p. 197).

Conclusions

Macrochirichthys macrochirus is a highly specialized piscivore derived from an ancestral lineage now represented by the genera *Salmostoma* and *Securicula*. These taxa are members of a monophyletic assemblage (the cheline group) in which three lineages can be recognized, viz. the cheline, represented by *Chela;* the oxygastrine, by *Macrochirichthys*, *Parachela* and *Oxygaster*, and the salmostomine by *Salmostoma* and *Securicula*. Parallelism between *Macrochirichthys* and *Securicula* has in the past led to the erroneous assumption of their close relationship (Bănărescu, 1967).

The Cultrinae (Bănărescu, 1967) have been shown to be a non-monophyletic assemblage although two groups of genera – the cultrine and hemicultrine – may be monophyletic. One of these is possibly the sister-group of the chelines.

Macrochirichthys is capable of a great degree of cranial elevation, made possible by the ball and socket connection of the basioccipital with the 1st vertebra and modifications of the epaxial musculature. Cranial elevation is also possible – perhaps to an even greater degree – in *Chela*. *Salmostoma* represents the plesiomorph lineage in which there are seen pre-adaptations to this function, namely, a short post-parietal area with a posteriorly rounded cranium and a reduced supraoccipital process; short ethmoid region overlapped by the frontals; rounding and shortening of the 1st vertebra with reduction of its lateral processes; a caudal inclination of the neural complex and modification of the anterior supraneurals. Such adaptations have resulted, on the one hand, in the evolution of forms such as *Macrochirichthys* and *Securicula* where the cranium is compressed and the dorsal musculature has extended across the skull roof; and on the other hand, in *Chela*, where the cranium has remained broad and there has been little modification to the dorsal muscle elements. Likewise, the protrusibility of the upper jaw is virtually lost in *Macrochirichthys* and *Securicula* but retained in *Chela*.

Further comparison between *Macrochirichthys* and the characoid *Rhaphiodon* has highlighted the major anatomical differences involved in achieving similar evolutionary status. It may be added here that a neck-bending mechanism similar to that of *Rhaphiodon* appears to be present in the siluroid *Belodontichthys* (pers. obs.).

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Miscellanea

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Siliceous structures secreted by members of the subclass Lobosia (Rhizopodea: Protozoa)

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Introduction

The need for a comprehensive taxonomic system for those amoebae with shells, usually referred to as testate amoebae, is long overdue. Nevertheless, before such a task is undertaken the valid criteria for each taxon should be established. The two main criteria used in recent classifications of testate amoebae in the Superclass Rhizopodea are the cytoplasmic form of the pseudopodia and the structure of the shell. The present study is concerned only with the latter, so the proposals concerning the mechanisms of pseudopodial movement suggested by Bovee & Jahn (1966) have not been considered. Furthermore, the changes put forward here are modifications of the classifications of Loeblich & Tappan (1961, 1964) and Deflandre (1953) – (referred to as the 'legally-based system' by Bovee & Jahn). In these classifications the shape and composition of the shell has been used to determine the divisions at the superfamily and family level. Four basic types of shell are recognized : first, the proteinaceous shell, usually composed of numerous alveoli; secondly, the agglutinate shell composed of extraneous material bound by an organic cement; thirdly, the siliceous shell usually composed of shell plates; and finally, the calcareous shell which may have an outer organic lining.

The divisions proposed here relate to the third type of shell structure, and concern those animals which make their own siliceous shell components. To date, that includes most of the species belonging to the subclass Filosia, and some species belonging to the subclass Lobosia, namely *Difflugia oviformis* Cash, 1909, *Quadrulella symmetrica* (Wallich, 1863) and *Lesquereusia spiralis* (Ehrenberg, 1840). Other testate amoebae in the subclass Lobosia which have siliceous plates, for example, species belonging to the genera *Nebela* and *Heleopera* have agglutinate shells, made of captured shell plates or quartz particles. The shell plates of smaller testate amoebae, such as *Euglypha*, *Assulina* and *Cyphoderia*, are easily recognized in the shells of *Nebela* species, and MacKinlay (1936) suggested that these were obtained by predation after observing that *Nebela collaris* produced a membranous shell devoid of shell plates when grown in isolation.

Discussion

It is generally accepted that all testate amoebae secrete an organic material that either provides the entire shell, as in *Arcella*, or at least is used to cement the shell components together as in, for example, *Nebela*, *Difflugia* and *Euglypha*. Fine structure studies (Hedley & Ogden, 1973, 1974*a*; Netzel, 1975, 1976*a*, 1977; Hedley *et al.*, 1976, 1977) on species belonging to all four of the basic shell types have shown that this organic material is made in the Golgi complex of the cytoplasm, and have suggested how it is probably used in shell construction. In addition, the cytoplasmic changes associated with the formation and distribution of siliceous structures in *Euglypha rotunda*, *E. acanthophora*, *E. strigosa*, *Trinema lineare* and *Difflugia oviformis* have been described in detail by Hedley & Ogden (1973, 1974*a*, *b*) and Netzel (1976*b*, 1977). These studies, based on laboratory cultures, include observations on the biology of these species, and cine-films illustrating binary fission have been made by Netzel (1971*a*, *b*). The siliceous structures secreted by *Euglypha* species and *Difflugia oviformis* are formed in a membrane-bound vesicle within the cytoplasm, and are stored there prior to division. At division, they are arranged around a cytoplasmic extrusion to form a daughter shell identical to the parent. The term 'idiosomes' has been suggested (Netzel, 1972) for the siliceous structures secreted by *Difflugia oviformis*.

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Using the diagnosis of the family Difflugiidae given by Loeblich & Tappan (1961, 1964), that the 'test is rarely chitinous, but is generally composed of foreign particles, not of secreted plates' and of the genus *Difflugia* – 'wall with pseudochitinous base and variable amounts of agglutinate material', it is apparent that *Difflugia oviformis* with its secreted shell does not agree with this definition. There would appear to be no justification in amending the diagnosis for an already overcrowded genus, instead it is proposed to create a new genus *Netzelia* to include *D. oviformis* and other species of *Difflugia* which secrete their own siliceous elements or idiosomes.

A similar situation arises in the family Hyalospheniidae. The diagnosis for this family states – 'test chitinous with siliceous plates or scales, rounded or angular, and may have foreign matter added'. Two of the genera included in this family are thought to secrete a proteinaceous shell, *Hyalosphenia* Stein, 1857 and *Leptochlamys* West, 1901, and two siliceous structures, *Quadrullella* Cockerell, 1909 and *Lesquereusia* Schlumberger, 1845. An ultrastructural study of *Hyalosphenia papilio* by Joyon & Charret (1962) suggested that it had a proteinaceous shell, but little is known about the shell of *Leptochlamys* except that it was originally described as having a thin chitinous membrane. Information on the shell of *Quadrulella* is still needed, although it is assumed that it secretes its own shell plates, because they have a distinct quadrangular shape (Fig. 1) which is restricted to this genus and *Paraquadrula* Deflandre, 1932 which has calcareous plates. Species belonging to *Quadrulella* have previously been described as having calcareous, siliceous or chitinoid shells (Cash & Hopkinson, 1909 ; 134–135). Elemental analysis of whole shells of *Q. symmetrica*, recently carried out in this laboratory using an energy dispersive X-ray analyser attached to a scanning electron microscope, have shown that they are composed mainly of silicon, with some potassium and calcium present. The amounts detected suggest that the shell plates are siliceous and that the organic cement which binds them may be strengthened by the other elements. The genus *Lesquereusia* contains several species whose shells are composed mainly of siliceous rods, three of these *L. epistomum*, *L. modesta* and *L. spiralis* have recently been redescribed (Ogden & Hedley, 1980) and only *L. modesta* consistently incorporates irregular foreign particles amongst the rods in the shell.

Although clonal cultures of *Lesquereusia spiralis* have not yet been established, observations of this species in isolation, in this laboratory, have shown that it secretes a daughter shell made of curved rods similar to those of the parent. Some of the laboratory specimens were smaller than those reported from the wild (see Ogden & Hedley, 1979), and this is thought to be due to a deficiency in the culture medium. A comparison between the curved rods of the smallest specimen, 83 µm (Fig. 2) those of a medium specimen, 95 µm (Figs 4 & 5) and a large specimen, 120 µm (Figs 6 & 7), show that these rods become more pronounced and areas of organic cement with the distinctive pores (Fig. 3) less numerous with increase in size. Elemental analysis of whole shells, using an energy dispersive X-ray analyser, has shown that these rods are siliceous and suggests that the organic cement that binds them contains iron.

The situation regarding the family Hyalospheniidae needs some clarification, but must await studies on clonal cultures before this is possible. However, it seems to me that there are sufficient affinities between *Lesquereusia spiralis*, *Quadrulella symmetrica* and the new genus *Netzelia* to

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Fig. 1 Siliceous shell plates of *Quadrulella symmetrica*. × 2400

Fig. 2 Shell surface of small specimen of *Lesquereusia spiralis*, to show the curved rods and pores. × 2100

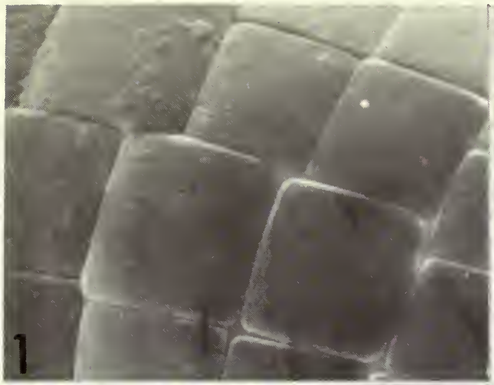
Fig. 3 A higher magnification of the pores in the organic cement, from the area arrowed in Fig. 2. × 21 000

Fig. 4 A medium-sized specimen of *L. spiralis* to show the ill-defined siliceous rods. × 490

Fig. 5 Portion of shell surface of medium specimen, note the numerous pores. × 8900

Fig. 6 Large specimen of *L. spiralis* with well-defined siliceous rods. × 480

Fig. 7 Shell surface of large specimen, note the apparent absence of pores. × 4800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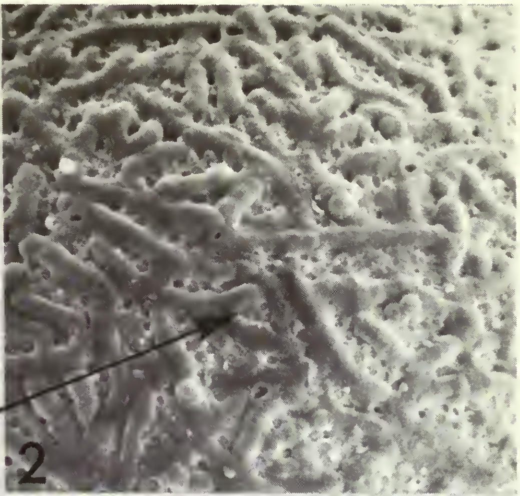
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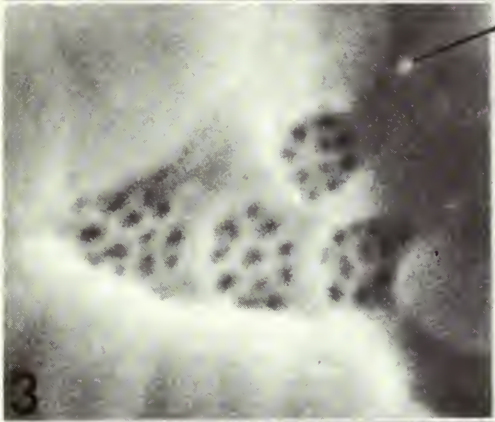
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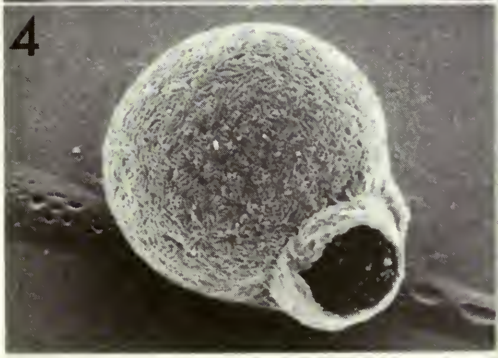
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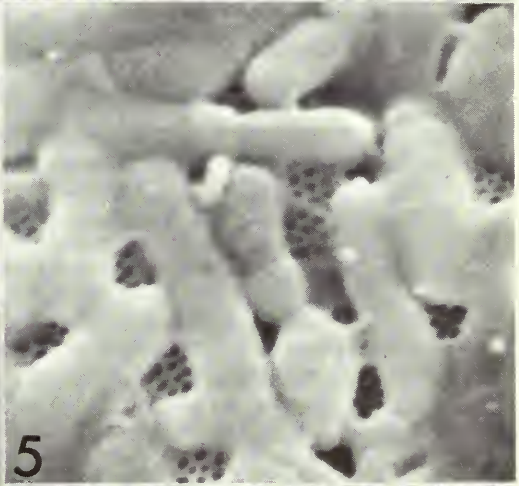
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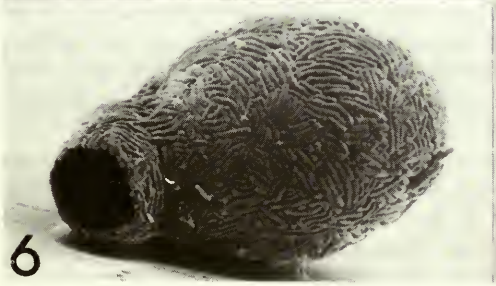
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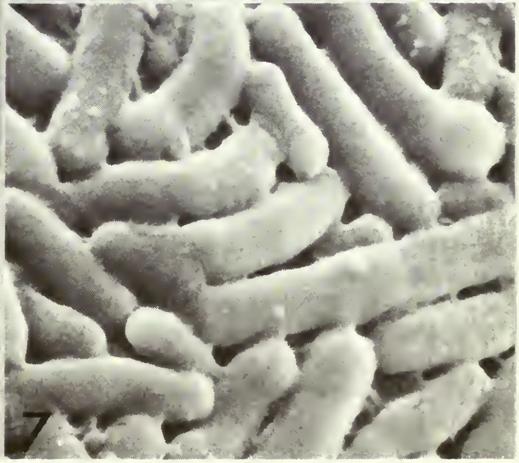
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warrant family status within the subclass Lobosia. I therefore propose to designate a family to accommodate these species by redefining Lesquereusiidae Jung, 1942, previously synonymized by Loeblich & Tappan (1961), to include those members of the subclass Lobosia which secrete siliceous elements.

Family **LESQUEREUSIIDAE** Jung, 1942 nom. rev.
[nom. correct pro Lecuereusiidae Jung, 1942]

Shell constructed of siliceous rods, plates or idiosomes secreted in the cytoplasm, to which mineral particles may be added; aperture circular, oval or elongate.

Lesquereusia Schlumberger, 1845. Shell colourless, compressed ovoid or globose with asymmetrical neck, giving the appearance of a spiral, composed of interwoven siliceous rods and sometimes particles of quartz; aperture circular.

to include: *Lesquereusia epistomum* Penard, 1902
Lesquereusia modesta Rhumbler, 1895
Lesquereusia spiralis (Ehrenberg, 1840)

Netzelia gen. n. Shell colourless, ovoid, symmetrical, with a broad crown and sides tapering smoothly to the aperture, composed of idiosomes but may incorporate grains of quartz; aperture circular, with organic collar and often with four or five small lobes.

to include: *Netzelia oviformis* (Cash, 1909) comb. n.

Quadrulella Cockerell, 1909. Shell colourless, ovoid, composed of quadrangular shell plates arranged without overlapping; aperture oval.
to include: *Quadrulella symmetrica* (Wallich, 1863).

In defining the above taxonomic changes, none of the generic names proposed by Jung (1942) in his review of the genus *Difflugia* have been considered, I agree with Deflandre (1953) and subsequent authors that these must be rejected as inadequate definitions.

It is apparent from previous descriptions of species of *Difflugia* that problems have arisen in identification due to differences of shell structure. For example, Penard (1902) described specimens similar to *Difflugia tuberculata* (Wallich, 1864) but having a thin, transparent shell without indentations. These specimens are listed by Jung (1942) as *Cingodifflugia laevis* (Penard, 1902). A species of *Difflugia* collected from water and mud in Alabama was tentatively identified by Owen & Jones (1976) as *D. tuberculata.* It produced autogenous siliceous components when isolated in culture, and Owen & Jones suggested that this species should therefore be referred to the genus *Nebela.* Their specimens do not agree with the accepted definition of *D. tuberculata*, which typically have distinctive tubercles of quartz grains on the shell surface (see Ogden & Hedley, 1979). However, this latter description may have to be amended because examination of specimens from the Everglades National Park, Florida, U.S.A. (kindly collected by Dr C. R. Curds, British Museum (Natural History)), suggest that *D. tuberculata* may occasionally construct a shell of diatom frustules instead of the usual quartz particles, both examples being present in the sample. Nevertheless, I consider that the descriptions of Penard (1902), Jung (1942) and Owen & Jones (1976) all refer to specimens of *Netzelia.*

It is probable that other smooth-shell species of *Difflugia* may secrete siliceous elements, although observations on such species in culture are needed. For example, the study of the shell structure of *Difflugia lobostoma* given by Eckert & McGee-Russell (1974) must be considered with caution, as I believe from their description that these authors were studying specimens of *D. tuberculata.* Nevertheless, the specimens examined were composed of a single layer of siliceous particles held together by a network of cement, and dense granules similar in structure to those seen in *Netzelia oviformis* by Netzel (1976*b*) were observed between the shell joints and in the cytoplasm.

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The first recorded specimens of the deep-water coral *Lophelia pertusa* (Linnaeus, 1758) from British waters

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Synopsis

Recognition of the deep-water coral *Lophelia pertusa* (Linnaeus, 1758) as part of the British fauna was based on four early nineteenth century specimens from Scottish waters, two from the Shetlands and two from the Inner Hebrides. These specimens have now been located and are figured. Each supports some epizoic remains including bryozoans, serpulid polychaetes, cirripedes and bivalves.

Introduction

During the early nineteenth century four specimens of the deep-water coral *Lophelia pertusa* (Linnaeus, 1758) were obtained by fishermen from Scottish waters. Two were from off the Shetland Islands and two from the Inner Hebrides. The specimens were mentioned by Johnston (1847) in the second edition of his work and later by Gosse (1860). They are important in that they are the earliest records of *Lophelia* from British waters.

Following Zibrowius (1976), the combination *Lophelia pertusa* (L.) will be used in this paper. The specimens were referred to as *Oculina prolifera* by Johnston (1847) and as *Lophohelia prolifera* by Gosse (1860).

The Shetland specimens

The precise collecting localities for the two Shetland specimens are not known. *Lophelia* does, however, occur on the edge of the Continental Shelf and the upper Continental Slope to the west and north of the Shetland Islands at depths of 190 m to approximately 300 m (Wilson, 1979*a*).

One specimen, perhaps the earliest recorded in British waters, was obtained by George C. Atkinson, possibly during a visit to Shetland in 1832 (Atkinson, 1838 : 223). He presented it to the then Newcastle Natural History Society (now, after several name changes, the Natural History Society of Northumbria) and it was placed in the Newcastle Museum (now the Hancock Museum, part of the University of Newcastle upon Tyne) (Johnston, 1847 : 252) in 1834 or 1835 (Natural History Society of Northumberland, 1838 : 423).

The coral collection in the Hancock Museum was examined by the author in 1974 and found to include only one specimen of *Lophelia* (Pl. 1A). The specimen was unlabelled. It is reasonable to assume that it is Atkinson's Shetland specimen, however, as it is 220 mm wide and 260 mm long. It can therefore be reconciled with the brief description given to Johnston by Joshua Alder that 'the specimen is eight or ten inches across' although dimensions alone clearly cannot positively identify the specimen. It weighs 2·1 kg.

This specimen shows the point of attachment to the substrate, and also records the early growth of the colony (Wilson, 1979*b*). The initial attachment was probably to an outcrop or large boulder and subsequent growth incorporated several adjacent small pebbles (Pl. 1A). Consideration of the form of the colony and the relative positions of the small pebbles on the sediment surface has enabled its probable orientation on the sea floor to be reconstructed (Fig. 1).

The specimen is clean in appearance and is largely free from epizoids over parts of its surface implying that it was partly covered by living tissue when collected. Evidence of attack by clionid

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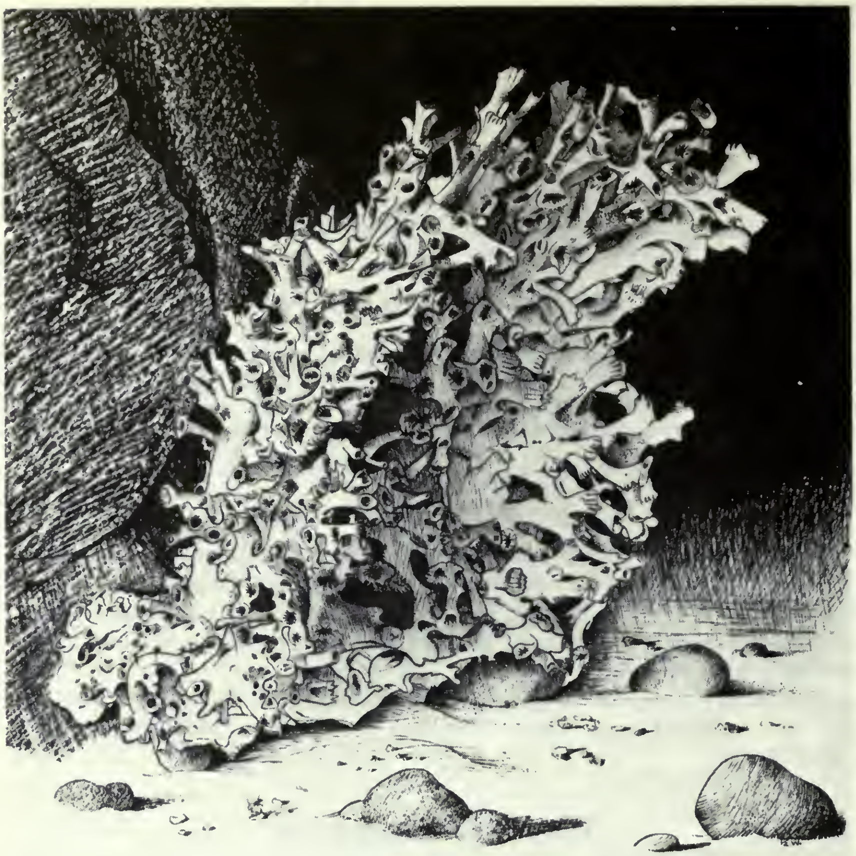

Fig. 1 Reconstruction of the probable orientation of the colony of *Lophelia pertusa*, in the Hancock Museum collection, on the sea floor. The initial attachment was probably to a large boulder or rock outcrop on the left. Subsequent lateral growth of the colony took place towards the right over the adjacent small pebbles on the sediment surface which became incorporated in the colony. Two of the four pebbles incorporated in this way (see Pl. 1A) are visible.

sponges is restricted to the 20–30 mm closest to the original point of attachment. Breakage did not occur above the point of attachment during collection because that part of the colony was only slightly weakened by the sponge borings. The specimen is therefore complete.

The epifauna included the bryozoans *Pyripora catenularia* (Fleming), *Amphiblestrum flemingii* (Busk), *Schizomavella* sp., *Sertella* sp., cf. *Oncousoecia dilatans* (Johnston), *Plagioecia patina* (Lamarck), *Diplosolen obelium* (Johnston) and *Disporella hispida* (Fleming); the barnacle *Verruca stroemia* (Müller); the polychaetes *Serpula vermicularis* (L.) and *Filograria* sp. and the bivalves *Heteranomia* sp. and *Hiatella* sp.

The other Shetland *Lophelia* was 'a very large specimen' (Johnston, 1847) obtained from Unst fishermen by Dr Laurence Edmonston, the Shetland naturalist, and given to J. Gwyn Jeffreys, who in turn presented it to the British Museum (Norman, 1869). Johnston was told of this specimen by Edward Forbes who, like Jeffreys, was a correspondent of Edmonston (Blaikie, 1888). Jeffreys visited Shetland in 1841 (Harrison, 1892) and it is possible that he was given the specimen then.

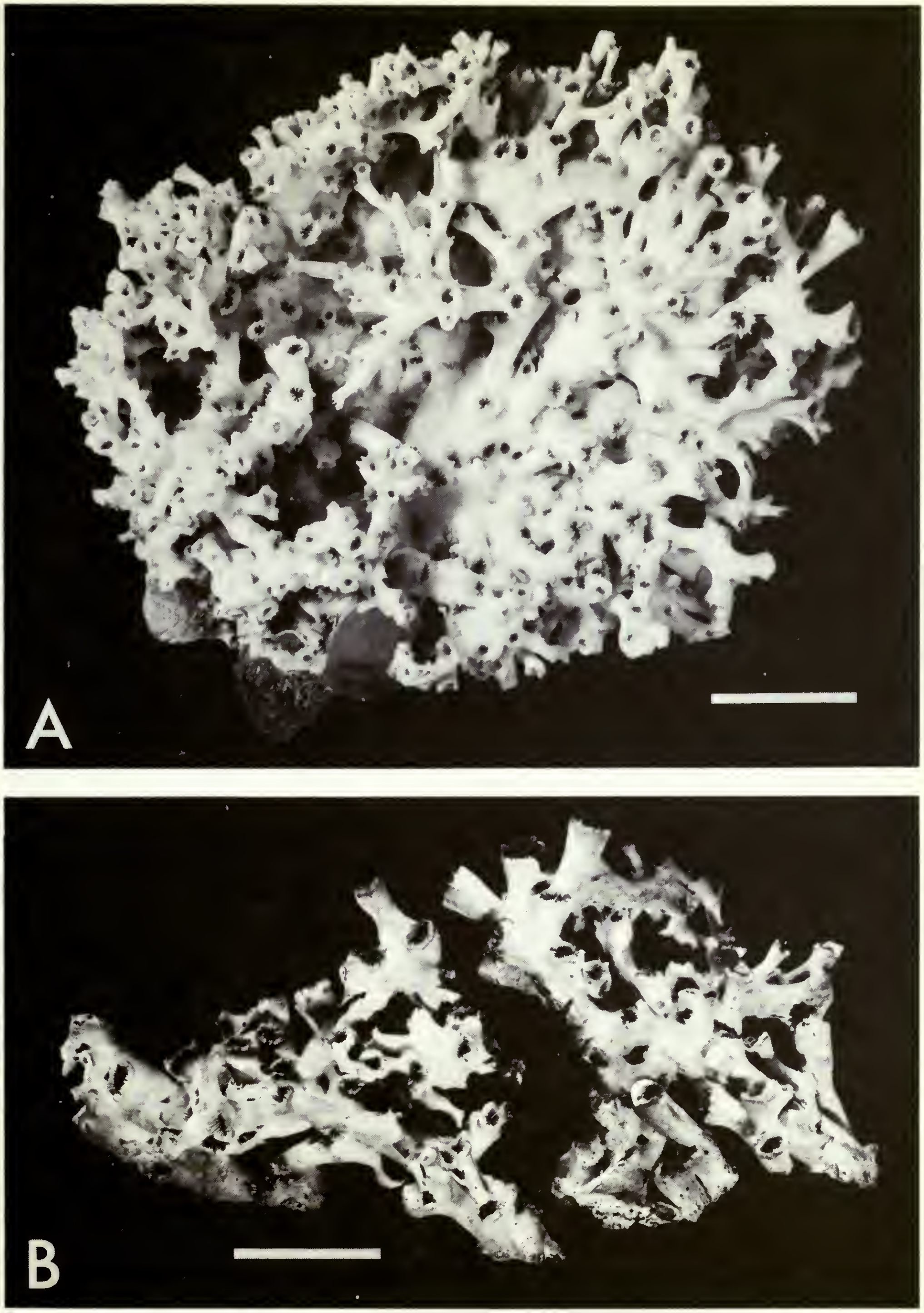

Plate 1 Specimens of *Lophelia pertusa* from off Shetland.

(A) Specimen probably obtained by George C. Atkinson and presented to the Newcastle Natural History Society. Hancock Museum collections. The pebbles covered by lateral growth of the colony are on the bottom left side of the specimen. Scale = 50 mm.

(B) Specimen (now in two pieces) obtained by Dr Laurence Edmonston from Unst fishermen and given to J. Gwyn Jeffreys. British Museum (Natural History) collections Reg. No. 1864.9.1.6. Note the clionid sponge borings on the bottom part of the right-hand portion. Scale = 50 mm.

A specimen of *L. pertusa* from Shetland presented by Jeffreys was registered in the British Museum collections in 1864 (BMNH Reg. No. 1864.9.1.6). As this is the only specimen in the collection from Shetland which was presented by Jeffreys it is probably Edmonston's specimen. It weighed 0·58 kg, and measured 260 mm by 140 mm. The specimen was broken many years ago and now exists as two pieces of approximately equal size (Pl. 1B).

The specimen incorporates several eunicid polychaete tubes and displays a fairly open growth form. The individual corallites at the extremities of growth are quite large, most being 15–17 mm in diameter. Parts of the specimen had been extensively bored by clionid sponges (Pl. 1B). The colony supported an epifauna including *Serpula vermicularis* and large colonies of the bryozoan *Turbicellepora* sp. One of the latter had a young colony of *Anarthropora monodon* Busk growing on it while another partially surrounds a *Serpula* tube. Boring Bryozoa were also present.

Although parts of the specimen are free from epifauna, the overall appearance suggests that the coral was dead when collected.

The Inner Hebridean specimens

Fleming (1846) recorded a specimen 2·72 kg ('6 lbs') in weight brought up by fishermen from the Sound of Rhum, between the islands of Rhum and Eigg, Inner Hebrides in 1845. Water depths of up to 160 m are to be found at the south-western end of the Sound. This specimen was exhibited at a meeting of the Royal Society of Edinburgh in 1846 and was referred to in a footnote in Johnston (1847 : 251–252). Gosse (1860), who was also told of this specimen by Professor G. Dickie, recorded it as having been deposited by Fleming in the Museum of King's College, Aberdeen. Ritchie (1912) considered that the specimen perhaps still existed as an unlabelled specimen in the Natural History Museum at Marischal College, Aberdeen. The British Museum (Natural History) collections contain a small specimen presented by Fleming, 9·6 g in weight (BMNH Reg. No. 1849.9.21.4) labelled:

> 'This is a fragment of the specimen "exhibited" by Dr Fleming at a meeting of the Royal Soc. of Edinr. 2nd March 1846, "6 pounds in weight, which was found last summer by fishermen, their lines having become entangled with it in the sea between the Islands of Rum and Egg" [sic] – Brit. Zooph. 252 – Presented by Dr Fleming.'

This small piece (Pl. 2A) was clearly broken off the large specimen sometime between 1845 (the year of collection) and 1849 (the year of accession to the British Museum). A large unlabelled specimen of *Lophelia* weighing 2·48 kg (5 lb 7 oz.), examined by the author in the University of Aberdeen Natural History Museum collections in 1977 (Reg. No. Coel 189 Z 2A) was thought perhaps to be the missing Sound of Rhum specimen. That this specimen is in fact the one exhibited by Fleming and referred to by Gosse has now been proved by reuniting the small piece in the British Museum (Natural History) collection to the point on the larger specimen from where it had been broken off (Pl. 2A).

The larger piece supported an epifauna including *Serpula vermicularis*, *Hydroides* sp., *Verruca stroemia* and bivalves including cf. *Heteranomia* sp., *Kellia suborbicularis* (Montagu) and *Hiatella* sp. Three species of Bryozoa – *Amphiblestrum flemingii* (Busk), *Porella concinna* (Busk) and *Plagioecia patina* (Lamarck) – were also fairly common, mostly as young colonies which had developed brooding structures. Boring Bryozoa were also present. Parts of the specimen had been extensively bored by clionids.

The growth form of the colony is very compact (Pl. 2A), in marked contrast to that of the Edmonston/Jeffreys specimen from Shetland. The individual corallites are also much smaller.

The small piece in the British Museum (Natural History) collections still has orange-pink coloration and has traces of dried tissue in the calices. Parts of the larger piece, particularly close to the point where the small piece was broken off, are clean in appearance, indicating that parts of this specimen were undoubtedly alive at the time of collection.

Gosse (1860) recorded and figured (pl. X) a specimen obtained by fishermen in deep water off Skye in 1852 and presented to Dickie. This specimen (Pl. 2B), which weighs 0·99 kg, was given in

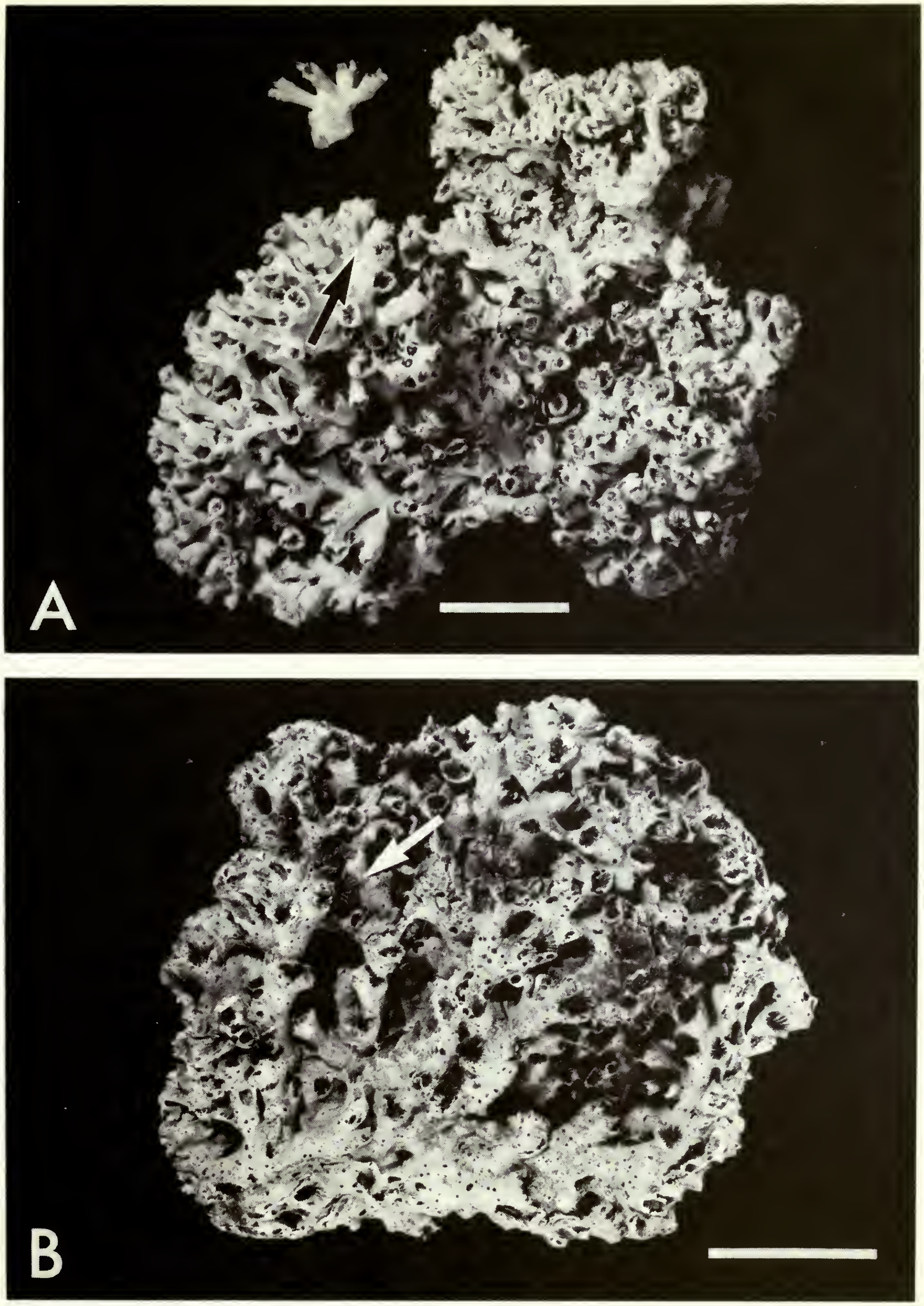

Plate 2 Specimens of *Lophelia pertusa* from the Inner Hebrides.

(A) Specimen obtained by fishermen from Sound of Rhum in 1845 and exhibited by Professor J. Fleming in 1846. The small piece in the top left-hand corner was broken off from the point indicated by the arrow and presented to the British Museum BMNH Reg. No. 1849.9.21.4. The large piece is in the University of Aberdeen Natural History Museum collections Reg. No. Coel 189 Z 2A. Scale = 50 mm.

(B) Specimen obtained by fishermen from off Skye in 1852 and given to Professor G. Dickie. National Museum of Ireland collections. Arrow indicates prominent *Caberea ellisii* colony. The coral is extensively bored by clionid sponges. Scale = 50 mm.

1869 by Dickie to A. G. More who was then an Assistant in the National Museum of Ireland, Dublin, and placed by him in the Museum collection (J. M. C. Holmes, personal communication). It is recorded as having been obtained 11 km (6 miles) west of Skye. Water of 145–190 m depth occurs in the Little Minch, 11 km west of Dunvegan Head, Skye, and it is possible that the specimen came from there. *Lophelia* was not recorded, however, during the British Association dredging investigations off Skye (Jeffreys, 1867; Norman, 1867).

This specimen supported a rich epifauna including *Serpula vermicularis*, *Hydroides* sp., *Verruca stroemia*, *Heteranomia* sp., *Modiolus phaseolinus* (Philippi), *Hiatella* sp. and *Crania anomala* (Müller). The bryozoan fauna was particularly rich and included *Amphiblestrum flemingii* (Busk), *Caberea ellisi* (Fleming) (see Pl. 2B), *Escharella ventricosa* (Hassall), *Schizomavella linearis* (Hassall), *Smittoidea reticulata* (J. Macgillivray), *Turbicellepora* sp., *Sertella* sp., *Stomatopora* cf. *trahens* (Couch), *Diplosolen obelium* (Johnston), *Disporella hispida* (Fleming) and *Lichenopora* cf. *radiata* (Audouin).

All the bryozoan colonies were small and some may have been only a few weeks old when the specimen was collected. A high proportion of these species had developed brooding structures.

The specimen also shows a compact growth form comparable with that of the Fleming specimen. It was extensively bored by clionid sponges. The remaining skeleton of the coral is grey in colour (see Gosse, pl. X) and was almost certainly completely dead when collected.

Recognition of *L. pertusa* as part of the British fauna

L. pertusa was not listed by Fleming (1828) or by Johnston (1838) in the first edition of his work. By the second edition (1847), Johnston knew of the two Shetland specimens and of Fleming's specimen and he suggested that *L. pertusa* should be included in the British fauna. It was not included by Forbes (1851) in his compilation of the early results of the British Association Dredging Committee investigations, although the section of this report dealing with the 'Zoophyta' (pp. 245–246) was based on records given by Johnston (1847).

By 1860, however, Gosse was able to figure Dickie's specimen in addition to recording the Fleming and Edmonston specimens and therefore to recognize *L. pertusa* as undoubtedly part of the British fauna. Gosse apparently did not make use of the footnote in Johnston (1847 : 251–252) as the important Atkinson specimen was not mentioned.

Further recognition of the species as British came when McAndrew (1861), using Gosse's data, included *L. pertusa* (as *Oculina prolifera*) in his check list of the British marine invertebrate fauna prepared for the Dredging Committee of the British Association, and subsequent authors have accepted it without comment.

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The British Museum (Natural History), London, the Hancock Museum, University of Newcastle upon Tyne, the National Museum of Ireland, Dublin and the Natural History Museum, University of Aberdeen are thanked for the loan of specimens described in this paper. Drs P. F. S. Cornelius, F. Evans, R. S. Thorpe, Messrs F. St P. D. Bunker, J. M. C. Holmes, A. P. Nimmo, K. R. Watt, Mrs A. Datta and Miss A. A. Kirkpatrick are thanked for their assistance in the search for the specimens and for details of their accession to the various museum collections.

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The larval and post-larval development of the brachyuran crab *Geryon tridens* Kröyer (Family Geryonidae) reared in the laboratory

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Synopsis

Four zoeal stages, a megalopal and first crab stage of the N.E. Atlantic crab *Geryon tridens* are described from laboratory reared material and compared with the corresponding stages of the N.W. Atlantic *G. quinquedens*. Diagnostic features are given for distinguishing the zoeae and megalopa of *G. tridens* from those of the portunid crabs and from *Goneplax rhomboides* occurring in British waters. The juvenile crab stages of *G. tridens* are compared with those of the southern Atlantic deep water *G. longipes*. The developmental stages of *G. tridens* suggest that *Geryon* evolved from the same phylogenetic stock as the Portunidae, Xanthidae and perhaps a part of the Goneplacidae.

Introduction

The crab *Geryon tridens* Kröyer has been recorded from the waters of northern Scandinavia, the northern North Sea and the N.E. Atlantic Ocean to just south of Ireland (Christiansen, 1969 : 85–86 and BM (NH) records). Further southward its distribution is uncertain as some authorities (Bouvier, 1940 : 269) have synonymized *G. tridens* with the southern *G. longipes* A. Milne Edwards, while Zariquiey Alvarez (1968 : 389) has maintained *G. longipes* as a valid species.

Only the pre-zoea and first zoea of *G. tridens* have been described previously from laboratory hatched specimens of a female collected south of Bergen, Norway (Brattegard & Sankarankutty, 1967). In April 1975 an ovigerous *G. tridens* was trawled in the North Sea and presented to the BM(NH) by Dr M. S. Rolfe. The hatched larvae were successfully reared to provide material for the following description of the complete larval development of this species.

Materials and Methods

The ovigerous specimen was taken in the Auk oil field region, about 150 miles off the Firth of Forth, between 56°20·1′ N : 02°07′ W and 56°24·0′ N : 02°04′ W, in an 8 m beam trawl worked at 85 m from the MAFF R.V. *Corella*. The female and reared material are deposited in the Collections of the Zoology Department, BM(NH), reg. nos 1976 : 4; 1978 : 176–189.

The larvae were reared using the methods described by Rice & Ingle (1975 : 104) and Ingle & Clark (1977). All material was fixed and stored in the preservative formulated by Steedman (1976 : 148) until studies had been completed and then transferred to 70% ethanol for permanent storage. Drawings and measurements were made with the aid of a *camera lucida* and some morphological details were confirmed by scanning electron microscopy. Measurements taken were:

(a) the distance between tips of dorsal and rostral spines (T.T.), (b) carapace length from between the eyes to the posterio-lateral carapace margin (C.L.).

Results

Hatching occurred between 5 and 6 May 1975; an average of 69 days elapsed between hatching and the appearance of first crab stages. A percentage of the hatch reached seventh and one

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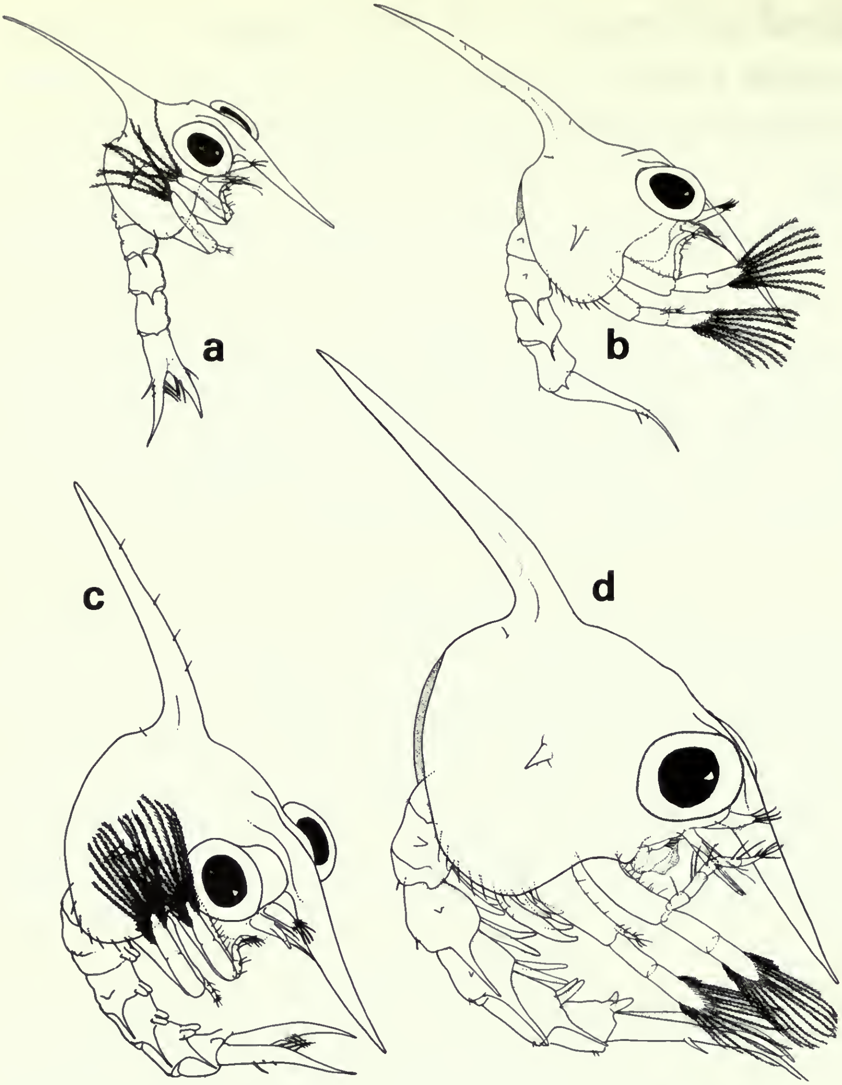

Fig. 1 *Geryon tridens*: zoeal stages (a) I, c.l. = 0·9 mm; (b) II, c.l. = 1·2 mm; (c) III, c.l. = 1·5 mm; (d) IV, c.l. = 2·0 mm.

specimen eighth, crab stage but further development was prevented by a failure of the air conditioning system.

Successfully reared larvae hatched as free swimming zoeae. Attempts were made to rear prezoeae liberated during the initial stages of hatching, but only one succeeded in developing to first zoea.

Descriptions

Geryon tridens Kröyer, 1837

Larval references: *Geryon tridens* Brattegard & Sankarankutty, 1967 : 7–12, figs 1–3 (prezoea, 1st zoea).

First zoea

DIMENSIONS. T.T. 2·6–2·8 mm; C.L. 0·8–0·9 mm.

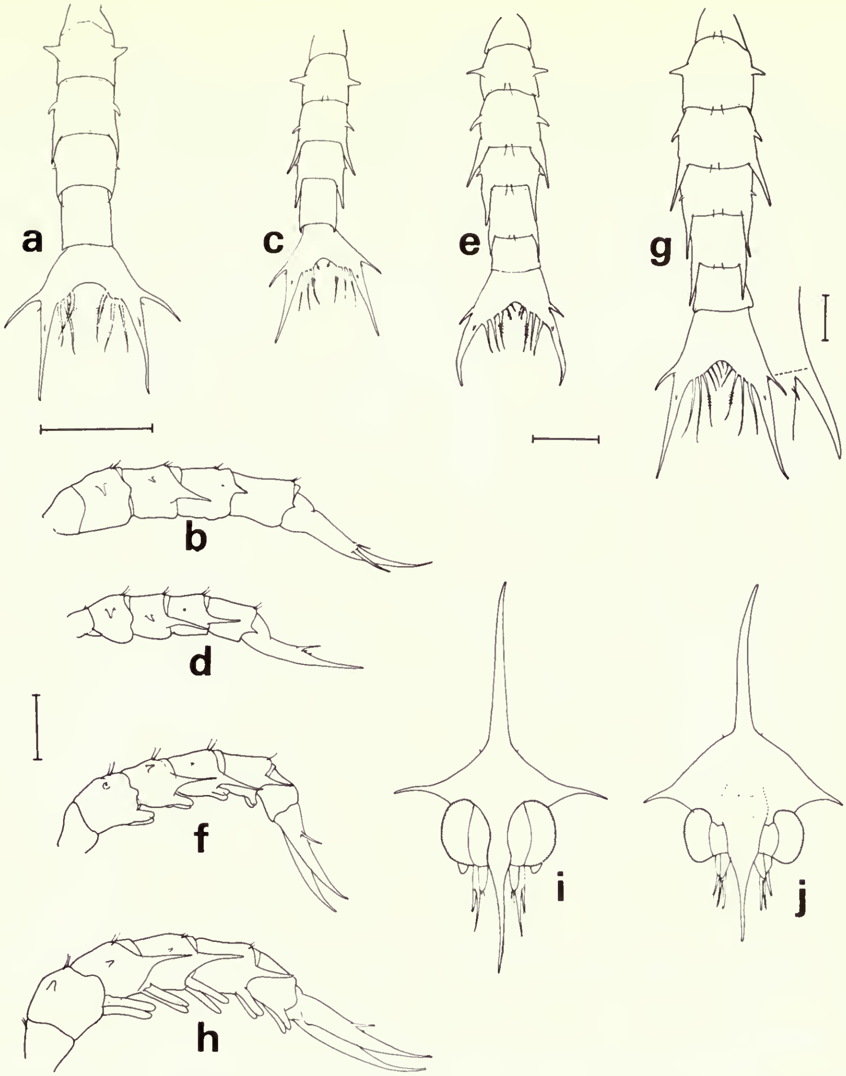

Fig. 2 *Geryon tridens*: abdomens of zoeal stages I–IV, dorsal (a), (c), (e), (g) and lateral (b), (d), (f), (h) aspects. Frontal aspects of (i) zoea I, (j) zoea IV. Scale = 0·5 mm, inset of (g) = 0·1 mm.

CARAPACE (Figs 1a, 2i). Dorsal spine well developed, straight, narrowing distally. Rostral spine straight, lateral spines long. Dorso-median elevation prominent. A pair of small dorso-lateral setae near base of dorsal spine. Posterio-lateral margin of carapace with a row of short spinules.

EYES. Partly fused to carapace.

ANTENNULE (Fig. 3a). Unsegmented, with two terminal aesthetascs and two short setae.

ANTENNA (Fig. 3f). Distal $\frac{1}{2}$–$\frac{2}{3}$ of spinous process spinulate; exopod not reaching into distal half of spinous process, with 2 terminal spines; endopod not developed.

MANDIBLE (Fig. 3k). Incisor and molar processes well developed, palp absent.

MAXILLULE (Fig. 4a). Endopod 2-segmented with 1, 6 setae respectively; basal endite with 4 setose spines and 2 setae; coxal endite with 9 setae.

MAXILLA (Fig. 5a). Endopod with large outer and small inner lobe with 5+3 setae; basal

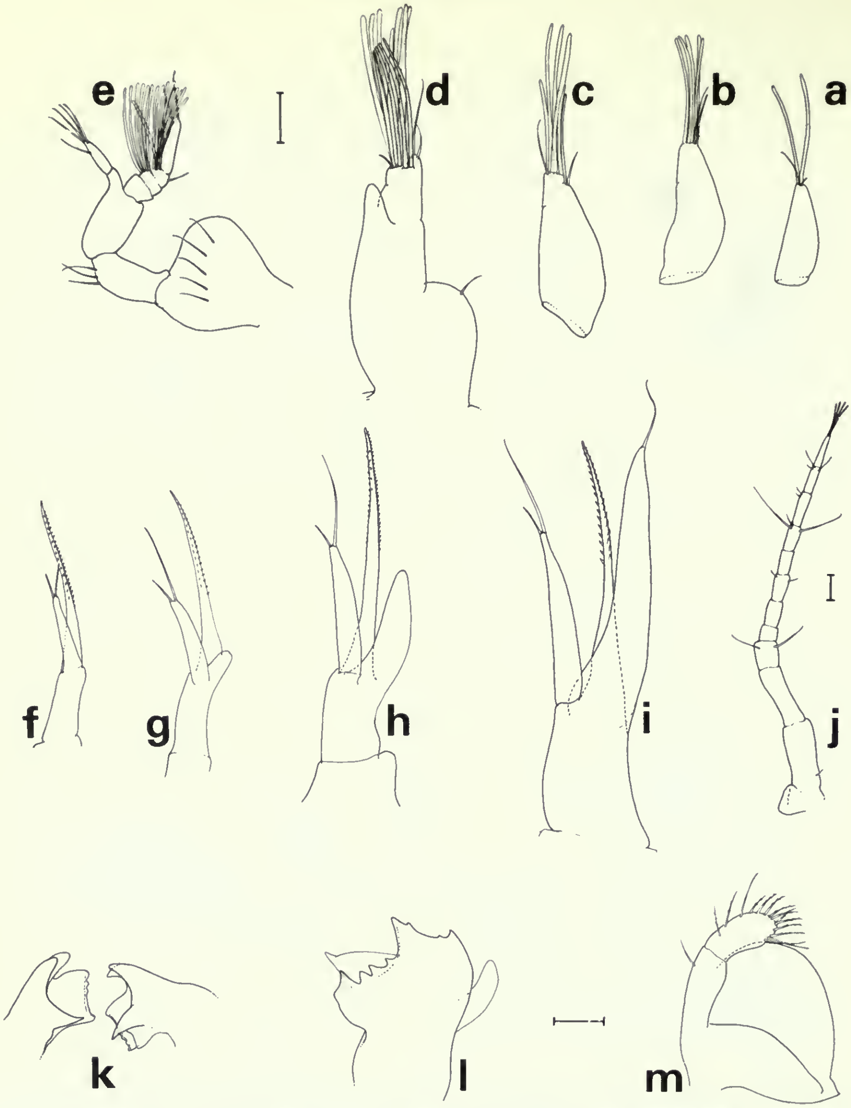

Fig. 3 *Geryon tridens*: antennules (a)–(d) of zoeae I–IV and (e) of megalopa. Antennae (f)–(i) of zoeae I–IV and (j) of megalopa. Mandibles (k) of zoeae I, (l) of zoea IV from ventral aspect and (m) of megalopa from dorsal aspect. Scales = 0·1 mm.

endite with large outer and small inner lobe with 6+5 setae; coxal endite bilobed with 4+3 setae; scaphognathite with 8 marginal setae and one long plumose posterior projection.

FIRST MAXILLIPED (Fig. 6a). Basis with 9–10 setae (arranged 2, 2, 3, 3); endopod 5-segmented with 2, 2, 1, 2, 4+1 setae; exopod incipiently 2-segmented with 4 terminal natatory setae.

SECOND MAXILLIPED (Fig. 7a). Basis with 4 setae; endopod 3-segmented with 1, 1, 5 setae; exopod incipiently 2-segmented with 4 terminal natatory setae.

THIRD MAXILLIPED AND PEREIOPODS. Represented as unsegmented buds.

ABDOMEN (Fig. 2a, b). 5-segmented+telson; 2nd segment with a pair of outwardly directed dorso-lateral processes; 3rd segment with a pair of smaller posteriorly curved dorso-lateral processes; 4th segment with a small pair of dorso-lateral spines. Posterio-lateral processes of

3rd to 5th segments decreasing in size on successive segments. A pair of minute setae near posterio-dorsal margin of each segment. Telson forks long, diverging posteriorly, with one long and one small lateral spine, dorsal spine well developed. Inner posterior margin of telson convex and with 3 pairs of long setae, innermost pair with long setules in middle section.

Second zoea

DIMENSIONS. T.T. 3·4–3·6 mm; C.L. 1·2–1·3 mm.

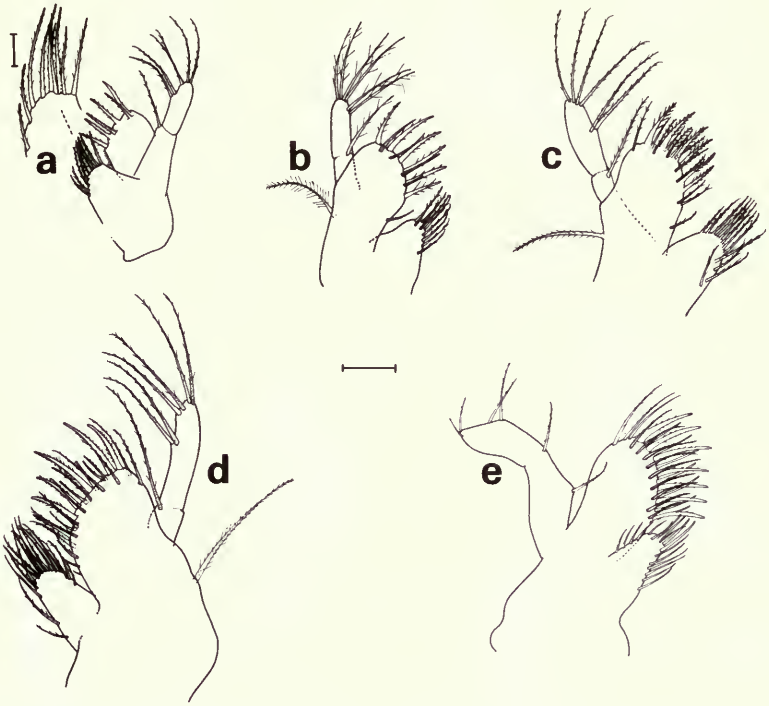

Fig. 4 *Geryon tridens*: maxillules (a)–(d) of zoeae I–IV and (e) of megalopa. Scale = 0·1 mm, inset to (a) = 0·03 mm.

CARAPACE (Fig. 1b). Considerably elevated in cross-section; dorsal spine sometimes with minute spinules; posterio-lateral margin with much longer spinules than in first stage.

EYES. Now stalked.

ANTENNULE (Fig. 3b). With 6 aesthetascs.

ANTENNA (Fig. 3g). Longer of the terminal spines on exopod much longer than in first stage: endopod bud well developed.

MANDIBLE. Unchanged.

MAXILLULE (Fig. 4b). Outer margin of basal endite with a prominent plumose seta, distal margin with 6 setose spines and 5 setae; coxal endite with 10–11 setae.

MAXILLA (Fig. 5b). Basal endite with 7+7 setae; coxal endite with 4+4 setae; scaphognathite with 18 marginal setae.

FIRST MAXILLIPED (Fig. 6b). Exopod with 9–10 terminal natatory setae.

SECOND MAXILLIPED (Fig. 7b). Distal segment of endopod with 6 setae; exopod with 9–10 terminal natatory setae.

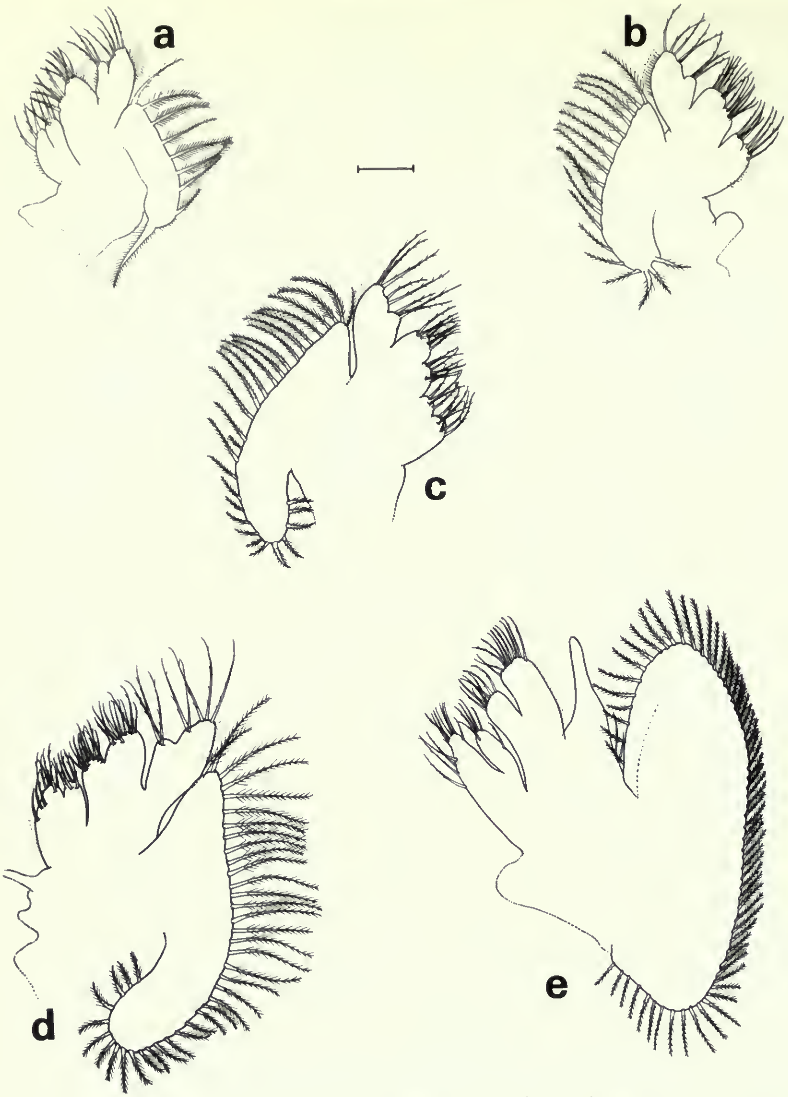

Fig. 5 *Geryon tridens*: maxillae (a)–(d) of zoeae I–IV and (e) of megalopa. Scale = 0·1 mm.

THIRD MAXILLIPED AND PEREIOPODS. Unsegmented buds larger than those of first stage.

ABDOMEN (Fig. 2c, d). Posterio-lateral processes longer than those in first stage. Inner margin of telson with 4 pairs of setae, innermost pair small.

Third zoea

DIMENSIONS. T.T. 4·0–4·2 mm; C.L. 1·5–1·6 mm.

CARAPACE (Fig. 1c). Dorsal spine stouter than in 2nd stage; setules prominent when present.

EYES Unchanged.

ANTENNULE (Fig. 3c). Setation unchanged.

ANTENNA (Fig. 3h). Exopod reaching into distal half of spinous process; endopod bud much longer than in 2nd stage.

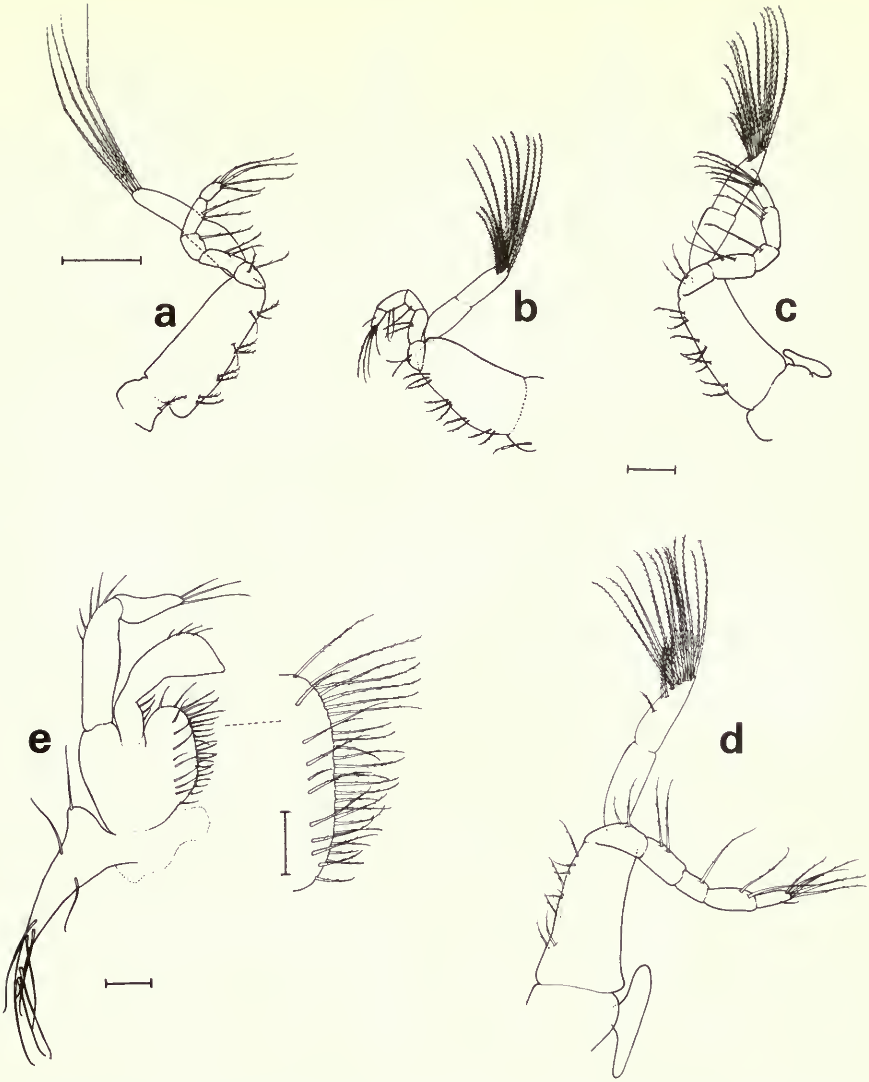

Fig. 6 *Geryon tridens*: 1st maxilipeds of (a)–(d) zoeae I–IV and (e) of megalopa. Scales = 0·2 mm except inset to (e) = 0·1 mm.

Mandible. Incisor and molar processes broader and serrate.

Maxillule (Fig. 4c). Basal endite with 12 setae; coxal endite with 12–13 setae.

Maxilla (Fig. 5c). Basal endite with 8+8 setae; coxal endite with 4+6 setae; scaphognathite with 25–29 setae.

First maxilliped (Fig. 6c). Coxa with prominent epipod; endopod distal segment with 5+1 setae; exopod with 12–14 terminal natatory setae.

Second maxilliped (Fig. 7c). Coxa with epipod; exopod with 12–14 terminal natatory setae.

Third maxilliped and pereiopods. Buds larger than those of 2nd stage.

Abdomen (Fig. 2e, f). 6-segmented; posterio-lateral processes, particularly of 4th–5th segments, longer than in 2nd stage. Pleopod buds developed, vestigial on 6th segment. Inner margin of telson with 5 pairs of setae (but sometimes with 6 setae on one side and 5 on other).

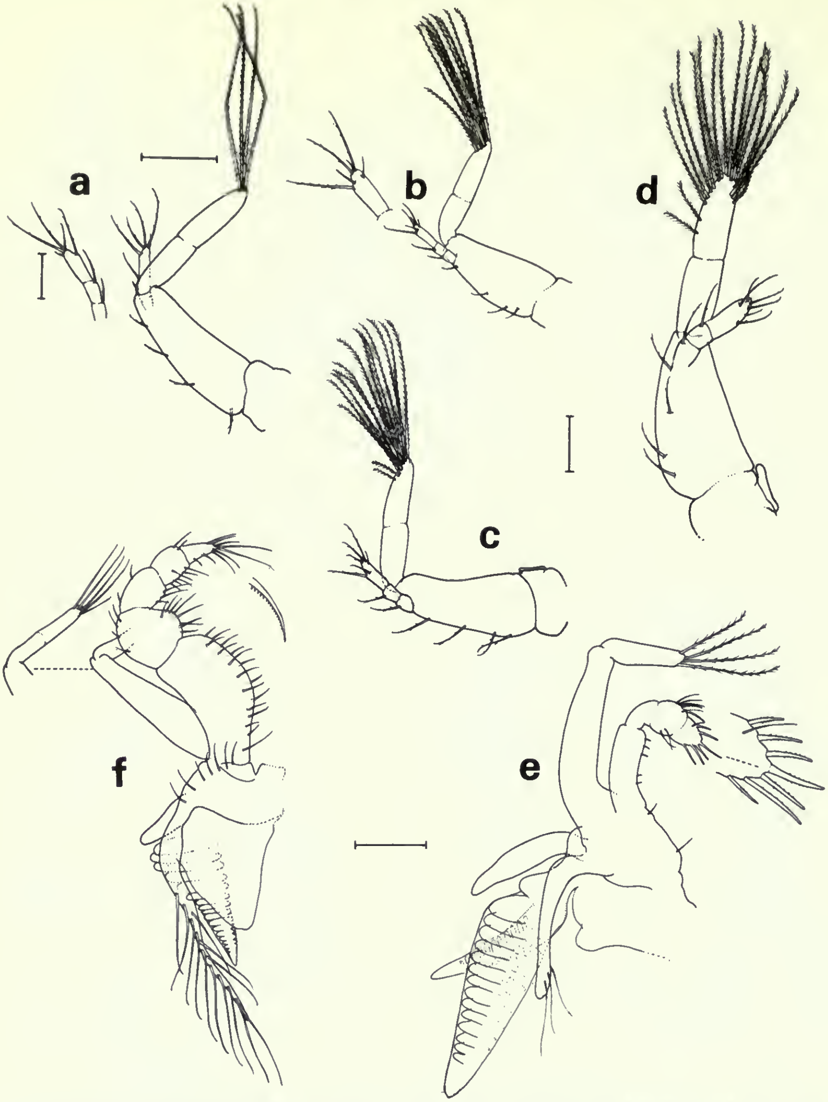

Fig. 7 *Geryon tridens*: 2nd maxillipeds of (a)–(d) zoeae I–IV and (e) of megalopa; (f) 3rd maxilliped of megalopa. Scales = 0·2 mm except insets to (a) and (b) = 0·1 mm.

Fourth zoea

DIMENSIONS. T.T. 4·9–5·2 mm; C.L. 1·8–2·0 mm.

CARAPACE (Figs 1d, 2j). Lateral spines slightly shorter than in 3rd stage.

EYES. Unchanged.

ANTENNULE (Fig. 3d). With 11 aesthetascs and 3 setae; endopod developed as a bud.

ANTENNA (Fig. 3i). Exopod reaching well into distal half of spinous process; endopod unsegmented, almost as long as spinous process and with a terminal seta.

MANDIBLE (Fig. 3l). With an unsegmented palp.

MAXILLULE (Fig. 4d). Basal endite with 18 setae; coxal endite with 17 setae.

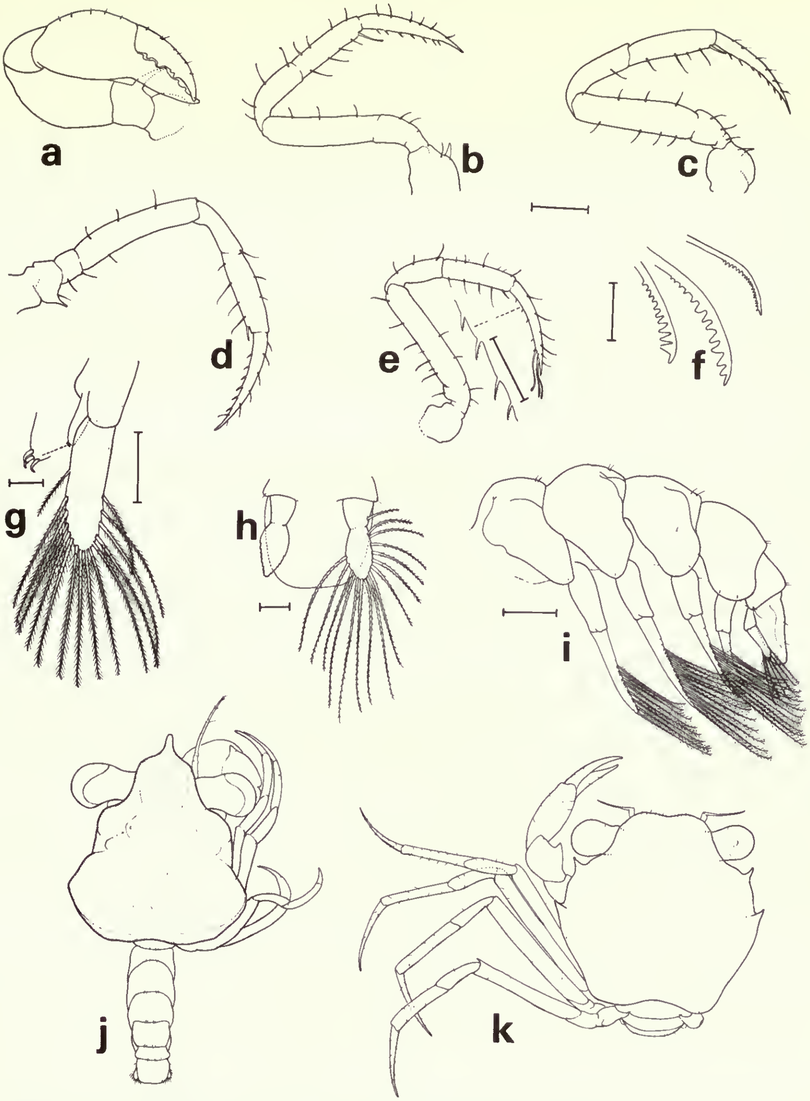

Fig. 8 *Geryon tridens*: megalopa (a)–(e) 1st to 5th pereiopods, scale = 0·5 mm, inset to (e) = 0·3 mm; (f) subterminal setae on dactylus of 5th pereiopod, scale = 0·05 mm; (g) 1st pleopod, scale = 0·3 mm, inset, scale = 0·05 mm; (h) telson and uropods, ventral aspect, scale = 0·1 mm; (i) abdomen, lateral aspect, scale = 0·5 mm; dorsal aspects of (j) megalopa c.l. = 3·0 mm and (k) 1st crab stage c.l. = 3·0 mm.

MAXILLA (Fig. 5d). Basal endite with 11 + 10 setae; coxal endite with 5 + 8 setae; scaphognathite with 40–42 setae.

FIRST MAXILLIPED (Fig. 6d). Coxal epipod longer than in 3rd stage; exopod with 16–17 terminal natatory setae.

SECOND MAXILLIPED (Fig. 7d). Coxal epipod larger than in 3rd stage; exopod with 17–18 terminal natatory setae.

THIRD MAXILLIPEDS. With a well developed exopod and 2 gill buds.

PEREIOPODS. Incipiently segmented, first pair chelate.

ABDOMEN (Fig. 2g, h). Smaller of 2 lateral spines on telson very reduced. Pleopod buds longer than in 3rd stage. Inner margin of telson with 6 pairs of setae.

Megalopa

DIMENSIONS. C.L. 3·0–3·1 mm.

CARAPACE (Fig. 8j) Longer than broad, narrowing anteriorly. Frontal region with a deep median furrow, rostrum deflected ventrally; each protogastric and inner epibranchial region with a small swelling; mesogastric region depressed; cardiac with a narrow and a broad U-shaped carina and one anteriorly placed tubercle on either side; intestinal region with a minute median tubercle.

EYES. Large and long, with well-developed cornea.

ANTENNULE (Fig. 3e). Peduncle 3-segmented, 1st segment with a row of transversely placed setae; 2nd segment with 3 disto-internal setae; exopod 4-segmented, 2nd segment with 6, 3rd with 10 aesthetascs and 2 setae respectively, 4th segment with 2 terminal setae; endopod segment with 4 terminal and 1 sub-terminal setae.

ANTENNA (Fig. 3j). Peduncle 3-segmented, 3rd segment with 2 long setae, flagellum 8-segmented, 3rd segment with 2 setae, 5th segment with 2 long and 1 short setae, 6th–7th segments with 2 and 3 setae respectively, 8th segment with 4 terminal aesthetascs.

MANDIBLE (Fig. 3m). Incisor process expanded as a broad concave plate with a sharp curved margin, molar process reduced; mandibular palp stout 2-segmented, proximal segment longer than distal with 1 disto-external setae, distal segment with 13–15 setae.

MAXILLULE (Fig. 4e). Endopod reduced but still with 6 setae; basal endite with 14 spines and 12–13 setae; coxal endite still with 17 setae.

MAXILLA (Fig. 5e). Endopod reduced, at the most with 2 outer basal setae; basal endite with 11+8 setae; coxal endite with 6+13–14 setae; scaphognathite with 62–63 setae.

FIRST MAXILLIPED (Fig. 6e). Exopod 2-segmented, proximal segment with 5 disto-external setae, distal segment with 3 terminal setae; basis with a longitudinal row of 23–25 marginal setae and a further row of 8–9 setae near inner margin of ventral surface; endopod indistinctly 2-segmented, terminally sub-acute with 3 setae on inner proximal margin and 4 setae on disto-outer margin; epipod well developed and with 10–12 setae.

SECOND MAXILLIPED (Fig. 7e). Coxa with 2–3 setae on inner margin; endopod 4-segmented, basal segment (merus) longest and with 5 small marginal setae, 3rd segment (propodus) with 2 spines and 6 setae, 4th segment (dactylus) with 7 spines and 1 seta; exopod 2-segmented, distal segment with 4 terminal setae; epipod bifurcate, longer and thinner part of bifurcation with several sub-terminal setae.

THIRD MAXILLIPED (Fig. 7f). Coxa/basis with a transverse row of setae; ischium inner margin with 17–25 setae, outer margin of merus with 3–4 setae, inner margin with 8–9 setae, carpal outer margin with 2 and inner with 3 setae respectively, propodal outer margin with 2 and inner with 7–8 setae, dactylus with 2 inner proximal and 7 terminal setae; exopod 3-segmented, distal segment with 5 terminal setae; epipod bifurcate, longer part setose.

PEREIOPODS (Figs 8a–e). Cheliped (a) stout and with a prominent ischio-basal spine; inner distal propodal margin and inner margin of dactylus with 3–4 blunt teeth. Pereiopods 2–5 (b–d) thin, inner margin of dactylus of each with 5–7 small spines, distal inner propodal margin with a spine, long on 2nd–3rd pereiopods; coxae of 2nd to 4th pereiopods each with a prominent spine, dactylus of 5th with 3 subterminal setae.

ABDOMEN (Figs 8i, j). With 6 segments+telson; posterio-lateral margins rounded and with 1–2 pairs of setae near dorso-lateral margin of each segment; telson slightly broader than long and with 2 pairs of median setae. Five pairs of pleopods, exopod of each with 15 marginal plumose setae on distal segment, basal segment of 5th (uropod) with a seta on outer margin; endopods of pleopods 1–4 with 3 distally placed coupling hooks.

First crab stage

Dimensions. C.L. 3·0–3·1 mm.

Carapace (Fig. 8k). Slightly longer than broad, frontal region with a longitudinal median furrow; antero-lateral margins each with 2 well-developed teeth.

Pereiopods (Fig. 8k). Cheliped moderately stout, carpal process acute. Pereiopods 2–5 long and thin, conspicuously setose.

Taxonomic remarks

The present laboratory reared material agrees with the account of the first zoea by Brattegard & Sankarankutty (1967) except in the following details.

	Brattegard & Sankarankutty	Present material
Total length:	2·0 mm	2·6–2·8 mm
Abdomen:	? Without setae near posterio-dorsal margin of segments 1–5	with a pair of setae on posterio-dorsal margins of segments 1–5
Antennule:	4 aesthetascs + 1 spinule	2 aesthetascs + 2 short setae
Mandible:	? undifferentiated	a clearly differentiated molar and incisor
Maxillule:	basal endite with 6 (5 in fig.) 'strong setae'; coxal endite with 7 setae	basal endite with 4 spines and 2 setae; coxal endite with 9 setae
Maxilla:	coxal endite with 10 setae; scaphognathite with 7 setae	coxal endite with 11 setae; scaphognathite with 8 setae

The complete larval development of only one other species of *Geryon* (the western Atlantic *G. quinquedens* Smith) has been previously described (Perkins, 1973). The zoeal stages of this species are noticably larger than those of *G. tridens* and dorso-lateral processes are usually developed on the fifth abdominal segment in *G. quinquedens*, whilst the pair on the fourth are much larger than the small spines on the corresponding segment of *G. tridens*. The posterio-lateral processes on the fifth segment of the abdomen are also much larger than those of *G. tridens*. The megalopa of *G. quinquedens* has only two subterminal setae on the dactylus of the fifth pereiopod compared with three present in *G. tridens*, and the exopods of the first to fifth pleopods are invested with 28 marginal setae whilst *G. tridens* has only 16. Further differences between the larvae of the two species are apparent when the setation of the appendages is compared as tabulated below.

	G. tridens	*G. quinquedens*
	First zoea	
Antennule:	2 aesthetascs + 2 setae	4 aesthetascs + 1 seta
Maxillule:	coxal endite 9 setae	coxal endite 6 setae
Maxilla:	basal endite 6 + 5 setae coxal endite 4 + 3 setae scaphognathite 8 setae	basal endite 5 + 5 setae coxal endite 3 + 3 setae scaphognathite 7 setae

	G. tridens	*G. quinquedens*
	Second zoea	
Antennule:	6 aesthetascs	4 aesthetascs
Maxillule:	basal endite 6 spines + 5 setae	12 spinous setae
Maxilla:	basal endite 7 + 7 setae scaphognathite 18 setae	basal endite 7 + 5 setae scaphognathite 22 setae
1st mxpd:	basis 8 setae	basis 10 setae
2nd mxpd:	distal endopod segment 6 setae	distal endopod segment 4 setae
	Third zoea	
Antennule:	6 aesthetascs + 2 setae	7 aesthetascs + 3 setae
Mandible:	palp not developed	palp developed
Maxillule:	basal endite 6 spines + 12 setae coxal endite 12–13 setae	basal endite 17 spinous setae coxal endite 17 setae
Maxilla:	basal endite 8 + 8 setae coxal endite 4 + 6 setae scaphognathite 25–29 setae	basal endite 7 + 5 setae coxal endite 5 + 9 setae scaphognathite 31 setae
	Fourth zoea	
Antennule:	11 aesthetascs + 3 setae endopod bud not setose	12 aesthetascs + 2 setae endopod bud setose
Maxillule:	basal endite 6 spines + 18 setae	basal endite 22 spinous setae
Maxilla:	basal endite 11 + 10 setae coxal endite 5 + 8 setae scaphognathite 40–42 setae	basal endite 12 + 9 setae coxal endite 5 + 9 setae scaphognathite 54 setae
2nd mxpd:	exopod 17–18 setae	exopod 19 setae
	Megalopa	
Maxillule:	endopod 6 setae basal endite 14 spines + 12–13 setae coxal endite 17 setae	endopod 4 setae basal endite 35 spinous setae coxal endite 25 setae
Maxilla:	endopod 2 basal setae; no lateral setae basal endite 11 + 8 setae coxal endite 6 + 13–14 setae scaphognathite 62–63 setae	endopod 3 basal setae; 8 lateral + 1 proximal setae basal endite 14 + 11 setae coxal endite 8 + 16 setae scaphognathite 100 setae
1st mxpd:	exopod, proximal segment 5 disto-external setae, terminal segment 3 setae basal endite 33–34 setae	exopod, proximal segment 6 disto-external setae, terminal segment 5 plumose setae basal endite 37 setae
2nd mxpd:	merus 5 marginal setae carpus without setae dactylus 7 spines + 1 setae proximal segment of exopod without setae	merus 3 marginal setae carpus 3 setae dactylus 10 setae (or spines) proximal segment of exopod with 4 marginal setae
3rd mxpd:	dactylus 9 setae exopod distal segment 5 setae	dactylus 12 setae exopod distal segment 6 setae

The zoeae of *G. tridens* can be readily distinguished from zoeae of all other brachyuran crabs reported from seas adjacent to the British Isles, except *Goneplax rhomboides* (Linnaeus), by the presence of dorso-lateral spines on the fourth segment of the abdomen. The features that separate *G. tridens* zoeae from those of *G. rhomboides* are tabulated below.

Zoeal features	*G. tridens*	*G. rhomboides* (after Lebour, 1928; Bourdillon-Casanova, 1960; Rice & Williamson, 1977)
Posterio-lateral margin of carapace:	with short spinules	with teeth and setae
Margins of posterio-lateral process of abdominal segments	unarmed	denticulate (see Bourdillon-Casanova, fig. 57a)
Telson forks:	unarmed two lateral spines on each fork in ZI–III	with minute spinules one lateral spine on each fork in all stages
Antennal exopod:	noticeably shorter than spinous process in early stages	almost, or as long as spinous process in early stages, shorter in later stages
Maxilla of ZIII:	scaphognathite with 25–29 setae	scaphognathite with 18–19 setae
1st maxilliped		
endopod setae of ZIII	2, 2, 1, 5+1	3, 2, 1, 2, 5,
exopod setae of ZI–IV	4, 9–10, 12–14, 17–18	4, 6, 8, 9–10
2nd maxilliped		
endopod setae of ZIII	1, 1, 6	1, 1, 5
exopod setae of ZI–IV	4, 9–10, 12–14, 16–17	4, 6–7, 8–9, 9–11

Megalopal features	*G. tridens*	*G. rhomboides*
Rostrum:	pointed	truncate
Carapace:	unarmed	with a pair of short protogastric spines

The large number (16) of marginal uropod setae distinguish the megalopa of *G. tridens* from those belonging to the genera *Polybius* (10 setae), *Macropipus* (8–10 setae), *Carcinus* (5 setae), *Xaiva* (10 setae) and *Portumnus* (7 setae). In addition, the dactylus of the 5th pereiopod is styliform in *G. tridens* but conspicuously lanceolate in megalopae of *Polybius*, *Macropipus* and *Portumnus*.

Juveniles of the deep water species *Geryon affinis* Milne Edwards & Bouvier have been occasionally misidentified as *G. tridens*. The dactyli of pereiopods 2–5 of *G. tridens* are strongly dorso-ventrally flattened whereas they are laterally compressed in *G. affinis*. This dorso-ventral flattening is apparent in *G. tridens* from the third crab stage (c.l. 5·0 mm) onwards, and may provide a means for separating the early post-larval stages of both species when corresponding stages of *G. affinis* become available for comparison.

The N. Atlantic *G. tridens* is replaced southward by the closely related *G. longipes* A. Milne Edwards. The larval stages of this species are unknown although the first zoeal stage of '*Bathynectes* sp. A' figured by Rice & Williamson (1977 : 47, fig. 22 a–d) is almost certainly a *Geryon* zoea and may be *G. longipes*. At present adults of both species can be separated only by differences in relative lengths of pereiopods 2–5 and by the degree of development of the antero-lateral carapace spines. In *G. tridens* the pereiopods are shorter and slightly stouter than those of *G. longipes* and the fifth is much less than twice the median length of the carapace. The antero-lateral carapace spines are also shorter, less spinose, and usually directed slightly more anteriorly than those of *G. longipes.* A comparison of the smallest juvenile of *G. longipes* (c.l. 17 mm, from the syntype series) with the largest reared crab of *G. tridens* (eighth stage c.l. 9·9 mm) has revealed that the limb/carapace ratios are the same for both species. However, the juvenile of *G. longipes* has the posterior pair of antero-lateral spines directed outward and set at an angle of a little less than 90° to the median axis of the carapace, whilst the corresponding pair of spines in *G. tridens* are directed forward as in the adult.

Brachyuran zoeae hitherto described from British waters, with few exceptions (*Ebalia*, Lebour, 1928 : 478; *Corystes*, Ingle & Rice, 1971 : 282), show regular increases of marginal setae on the exopods of the first and second maxillipeds (e.g. ZI 4 setae, ZII 6, ZIII 8, ZIV 10 and ZV 12 setae, respectively). The zoeae of *G. tridens* do not conform to this pattern as laboratory reared material show the following succession of setal development and variation — ZII 9–10 setae, ZIII 12–14, ZIV 16–18 setae. Irregular developmental sequences of exopod setae are, however, not unusual and occur in zoeae of the western Atlantic *G. quinquedens* and in some portunids (*Callinectes sapidus*, Costlow & Bookhout, 1959 and *Ovalipes ocellatus*, Costlow & Bookhout, 1966). In these species the exopod setal formulae differ sufficiently on either one pair, or on both pairs of maxillipeds, from one moult to the next to enable recognition of the individual zoeal stages.

Phylogenetic relationships

The larvae of *G. tridens* possess many portunid features (family Portunidae). In particular, the zoeae have long, relatively non-spinulate rostral and dorsal spines, outwardly directed long lateral carapace spines, a well-developed antennal exopod that is shorter than the spinous process, well-developed dorso-lateral processes on abdominal segments 2–3, a telson with three spinules on each fork (with the smallest one becoming reduced in later stages), the first maxilliped with two setae on the endopod first segment and the distal setae on the endopod of the maxilla arranged in three distinct groups.

Larval characters separating the three subfamilies of the Portunidae represented in British waters were given by Rice & Ingle (1975*a* : 148–149). Although the larvae of *G. tridens* do not possess all the characters listed for any one of these three subfamilies they show, nevertheless, strong affinities to the Polybiinae. The zoeae have the third segment of the endopod of the first maxilliped armed with a seta and well-developed lateral spines on the carapace, whilst the megalopa is without sternal cornuae, but has coxal spines on pereiopods 2–4 with a downward pointing rostrum, and the dorsal surface of the carapace is without spines or conspicuous processes.

Zoeae belonging to the Portunidae have dorso-lateral processes on abdominal segments 2–3, although they may disappear from the third segment in later stages; only exceptionally are these processes present on segments 4–5 (e.g. *Ovalipes*, Costlow & Bookhout, 1966, fig. 1a). These dorso-lateral processes are frequently well developed on the posterior abdominal segments of zoeae belonging to the families Xanthidae (e.g. *Menippe*, Porter, 1960, fig. 2u; *Panopeus*, Lebour, 1944, fig. 9 and *Eriphia*, Bourdillon-Casanova, 1960, fig. 55), the Goneplacidae (e.g. *Goneplax*, Lebour, 1928, Pl. XI, fig. 10; XII, fig. 1) and Grapsidae (*Plagusia*, Aikawa, 1937, fig. 35). The zoeae of *Menippe* and of *Goneplax* also have long posterio-lateral abdominal spines.

The zoeae of *G. tridens* possess a small but conspicuous pair of dorso-lateral processes on the fourth abdominal segment and, in later stages, the posterio-lateral spines are well developed on the second to fourth segment. In both features *G. tridens* shows affinities to the Xanthidae and Goneplacidae, whilst the first crab stage strongly resembles juveniles of the Goneplacidae (e.g. perhaps *Homoioplax* and *Psopheticus*) in having a sub-quadrate carapace with two antero-lateral teeth and long thin pereiopods, features that are not typical of the early post-larval stages of either xanthids or portunids.

The genus *Geryon* was assigned to the family Goneplacidae by Rathbun (1937 : 265), Sakai

(1939 : 554–555) and by Barnard (1950 : 282), but Bouvier (1940 : 261) placed in into the family Xanthidae. Colosi (1924), however, had already established the family Geryonidae for *Geryon* Kröyer, 1837 and the fossil genus *Archaeogeryon*. Balss (1957 : 1654) placed the Geryonidae between the Xanthidae and Goneplacidae. Boyden (1943) demonstrated serological affinities between *Geryon quinquedens* and a species of the family Xanthidae (*Menippe*) and Leone (1951) between species of Xanthidae and Portunidae (*Macropipus puber*), but these authors were not able to compare it with species in the Goneplacidae. Perkins (1973) also suggested that the larvae of *G. quinquedens* shared many features with those larvae in the family Xanthidae. The present study of the larval development of *G. tridens* supports this serological evidence and suggests that the Geryonidae may have been derived from the same phylogenetic stock as the Portunidae, Xanthidae and perhaps a part of the heterogenous Goneplacidae.

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Notes on the types of scorpions in the British Museum (Natural History), London
Buthus socotrensis Pocock, 1889 (Family: Buthidae)

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Résumé

L'étude des syntypes de *Buthus socotrensis* Pocock et de spécimens conservés au British Museum (Natural History) et au Muséum national d'Histoire naturelle de Paris confirme la validité de cette espèce jusqu'alors non retenue par les Spécialistes. *Buthus socotrensis* doit être placé dans le genre *Buthotus* Vachon, 1949, mais les caractères particuliers de sa trichobothriotaxie nécessitent la création d'un nouveau sous-genre: *Balfourianus*, création confirmant l'endémisme de la faune scorpionique de l'île Socotra.

Introduction

Buthus socotrensis was first described by R. I. Pocock in 1889 on the examination of four specimens collected from Socotra Island by Prof. B. Balfour. The description was then completed by Pocock in 1903. His new diagnosis corroborated K. Kraepelin's statement (1899) concerning the classification of the species in the *hottentota*-group of the genus *Buthus*.

In 1914, A. Birula, studying specimens collected by Franz Werner from North Africa, re-examined the species belonging to Kraepelin's *hottentota*-group (which he considered of sub-generic value). As noted by Pocock *Buthus socotrensis* is not referable to the sub-genus but must be placed close to *Buthus acutecarinatus* Simon, 1883 and *B. gibbosus* Brullé, 1832.

Pocock's species *socotrensis* was omitted from our revision of the family Buthidae and its classification was considered to be uncertain (Vachon & Stockmann, 1968).

On the basis of the study of four specimens belonging to the type-series and kept in the British Museum (Nat. Hist.) and of specimens from Socotra Island, deposited either in the Muséum national d'Histoire naturelle Paris (M.N.H.N.) or in the British Museum (B.M.), *socotrensis* could be referred to the genus *Buthotus* Vachon, 1949; nevertheless, a new name becomes necessary for the new sub-genus. *Balfourianus*, named after the first collector of the species: Prof. Baillie Balfour, is thus proposed.

Material examined

Consists of 11 females, three of these belonging to the type-series, Prof. T. B. Balfour, B.M. reg. no. 18, 81–106:

1 female lectotype (B.M.), registered as VA 1621–1. Among the four specimens studied by R. I. Pocock, none has been designated as the type; therefore, the female, the measurements of which correspond to the specimen originally described by R. I. Pocock (*loc. cit.*, 1889 : 339) has been designated as the lectotype.

2 female paralectotypes (B.M.): VA 1621–2 and VA 1621–3.

3 females (B.M.): VA 1218, VA 1220, VA 1222, Oxford University Exp., Hadibu Plain, 22.ix.1956, Socotra Island.

1 female (B.M.): VA 1695, Oxford University Exp., August 1956, Adho Dimellus, only under rock in damp areas, Socotra Island.

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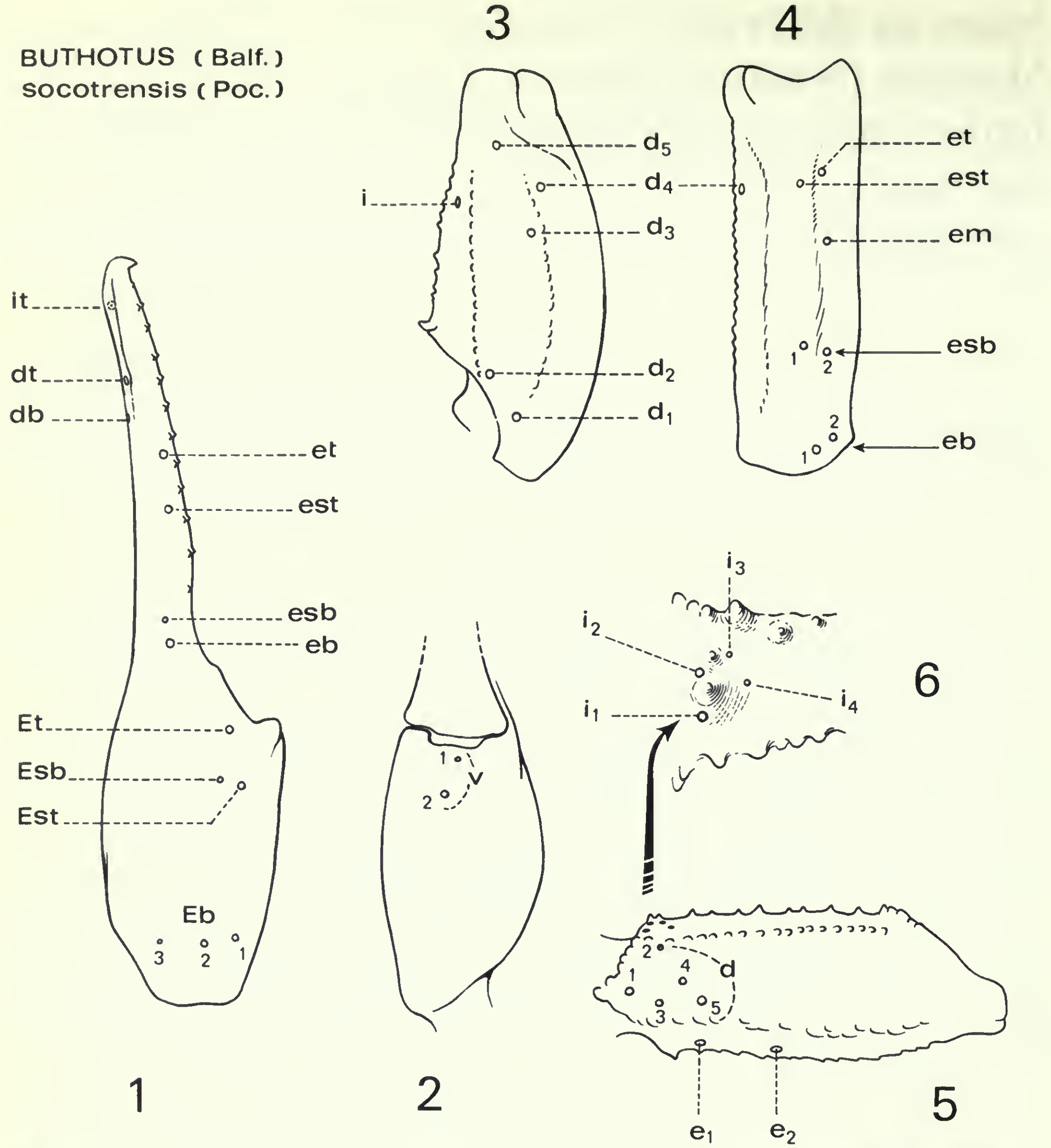
BUTHOTUS (Balf.)
socotrensis (Poc.)
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Figs 1 to 6 Right pedipalp of female paralectotype: VA 1621–2. 1, external side of chela; 2, ventral side of hand; 3, dorsal side of tibia (=forearm); 4, external side of tibia; 5, dorsal side of femur (=arm); basal area of internal side of femur. Only the trichobothries have been figured.

1 female (B.M.): VA 1224, Socotra Island, 10.x.1956; Zool. Soc. Lond. leg.

2 females (M.N.H.N.P.): RS 4684, RS 4687, Socotra Island, Hadibu Plain, K. M. Guichard leg. 1967.

1 female (M.N.H.N.P.): RS 4686, Socotra Island, sea level, K. M. Guichard leg. 1967.

and of 7 males:

1 male paralectotype (B.M.): VA 1621–4, Socotra Island, T. B. Balfour, 81–106.

1 male (B.M.): VA 1219, Zool. Soc. Lond. leg, 10.x.1956, Socotra Island.

3 males (B.M.): VA 1221, VA 1225, VA 1226; Oxford Univ. Exp., 1956; Socotra Island.

1 male (M.N.H.N.P.): RS 4685, Socotra Island, 28.iv.1967, Kalansya under palm fronds; K. M. Guichard leg.

The study of these 17 specimens fully supports the existence of the characters given in Pocock's diagnosis. Some data concerning the trichobothriotaxy, the chaetotaxy, the caudal keels and the pectinal teeth number will supplement the original diagnosis.

Trichobothriotaxy (Figs 1 to 6)
It agrees with our description of the *Buthotus*-genus (*loc. cit.*, 1949 : 145) but differs from it in that the trichobothry *db* is always distal to *et* (Figs 1 to 8) instead of basal (Fig. 7). This '*invariant*' disposition, i.e. unrelated to the sex or to the age of the specimen, is a taxonomic character of primary importance in easily discriminating between the Socotra Island species and the other known *Buthotus* species. On the basis of the relative positioning of the trichobothries *et*, *est*, *dt*, *db*, two sub-genera could be recognized in the genus *Isometrus* H. and E. (Vachon, 1972); in our revision of the genus *Lychas* C. L. Koch, this character has also been used.

Chaetotaxy
Among all the specimens examined, numerous and short setae, together with tergal ones, could be observed on the pedipalps (Polytrichy). The caudal segments only bear few setae, symmetrically arranged (Oligotrichy).

Caudal keels (metasoma)
According to R. I. Pocock (1903), because of the presence of a paired keel on the upper surface of the segment, the fourth segment bears 12 keels (which is unusual). Its existence could be settled. The keel consists of a row of granulae which may also occur (but less regularly) on the dorsal groove of almost all the segments, including the last one. It seems not to be a 'true 'keel.

Number of pectinal teeth
In R. I. Pocock's diagnosis (*loc. cit.*, 1889 : 339) the sex of the specimens examined could not be ascertained; neither was it stated whether the numbers indicated (24–25; 28–29) deal with individual variations or with sexual ones. But, in 1903, the sexual origin of the variations could be stated, the pectines of the female bearing 24 or 25 teeth, whereas in males, they are 28 or 29.

The sex of the 18 specimens at our disposal (11 females and 7 males) could easily be identified.

The following combinations could be noted:
in females: 23–25 (1 time); 25–24 (2 times); 25–25 (4 times); 26–25 (2 times);
in males: 27–28 (1 time); 28–29 (1 time); 29–28 (1 time); 30–31 (1 time); 31–31 (1 time); 31–32 (1 time); 32–30 (1 time).

It may be pointed out that:

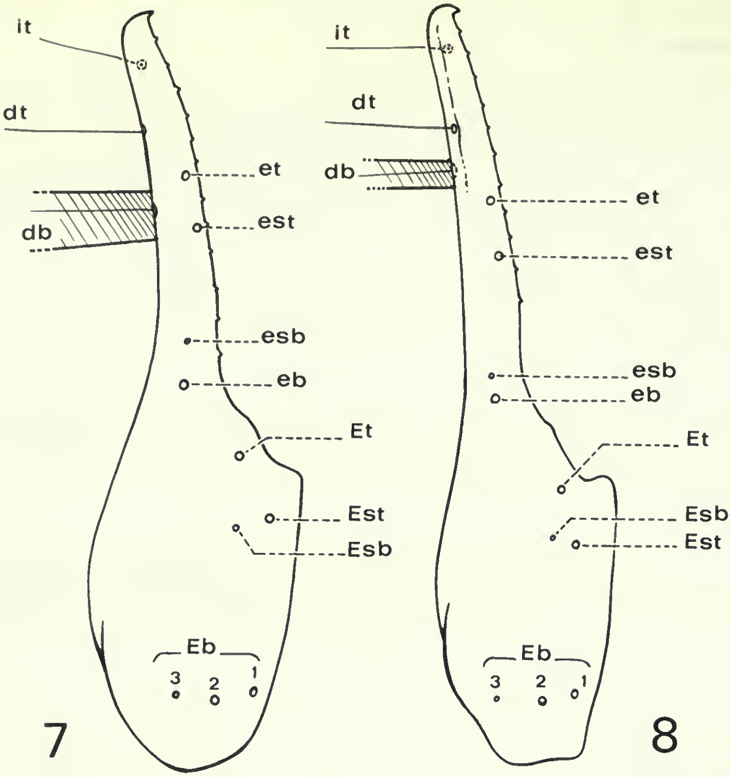
1. The number of pectinal teeth is a character of importance in discriminating between the sexes owing to the fact that in females it varies from 23 to 25, instead of from 27 to 32 in males.

2. The asymmetry is frequent, the number of teeth on the left side of a specimen differing from that found on the right one. Thus, of the 11 pairs of female pectines examined 7 are asymmetrical and in males, 6 of the 7 pairs of pectines are assymmetrical too.

3. The number 25 (referred to as type-number) is more frequently observed in females (15 of the 22 pectines examined); in males, owing to the small number (7) of specimens available, it could not be ascertained, But it may be noted that the arithmetical mean of the teeth number on each pectine is 29 ($\frac{407}{14}$).

Conclusions

1. On the basis of its trichobothriotaxy, *Buthotus socotrensis* may be easily separated from the other known *Buthotus* sp. It permits recognition of two sub-genera in the genus *Buthotus* Vachon, 1949: *Balfourianus* s.g. nov., to which the species *socotrensis* Pocock, 1889 may be referred and the type-subgenus: *Buthotus*, which for the moment includes the other known species.



Figs 7 and 8 Right chela. 7, in *Buthotus* (*Buthotus*) sp.; 8, in *Buthotus* (*Balfourianus*) *socotrensis* (Pocock). The 'territory' on which the position of *db* varies (according to species or to specimens belonging to the same sub-genus) is hachured.

Therefore, the generic diagnosis published in 1949 should be slightly modified according to the remarks published in 1968 (Vachon & Stockmann, *loc. cit.* : 89).

Revised diagnosis of the genus *Buthotus* Vachon, 1949

Concerning the positioning of the trichobothry *db* on the fixed finger, it may be noted that *db* is on the distal half of the finger but its position varies; it may be distal to *et* or between *et* and *est* or slightly basal to *est*.

Diagnosis of the nominal subgenus: *Buthotus* (*Buthotus*)

Characters very similar to those of the sub-genus but the trichobothry *db* is *always basal* to *et*.

Diagnosis of the new subgenus *Buthotus* (*Balfourianus*)

Characters very similar to those of the sub-genus but *db* is *always distal* to *et*.
The two sub-genera may be separated by means of the following key:

Fixed finger with *db* clearly distal to *et* (Figs 1 and 8) so that *dt* and *db* are both distal to *et* . . . . s.g. nov. *Balfourianus*
Type: *B.* (*B.*) *socotrensis* (Pocock, 1889); Socotra Island.

db between *et* and *est* or slightly basal to *est* (Fig. 7) . . . . s.g. *Buthotus*
Type: *B.* (*B.*) *judaicus* (Simon, 1872); Africa and Asia.

2. Endemism could be ascertained from the existence of a sub-genus and of a species of *Buthotus* occurring in Socotra Island as might be inferred from the presence of two other species which

have never been collected elsewhere: *Hemiscorpion socotranus* Pocock, 1889 (Fam. Scorpionidae) and *Butheolus insularis* Pocock, 1889 (Fam. Buthidae).*

It may be noted that an endemic genus, *Heteronebo* Pocock, 1889, could be observed in Abd-el-Kuri, a small island between Gardafui Cape and Socotra Island; two species: *H. granti* Pocock, 1889 and *H. forbesii* Pocock, 1889 are assignable to the genus (Fam. Diplocentridae). The genus has never been collected from Somalia, from Socotra or from Arabia (O. F. Francke, 1977).

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*O. F. Francke (1977) points out the presence of three endemic species on Socotra Island: *Hemiscorpion socotranus* Pocock (Scorpionidae), *Butheolus insularis* Pocock (Buthidae) and *Orthochirus socotrensis* Pocock (Buthidae). *Buthotus socotrensis* (Pocock) is not mentioned. On our part, we have no data concerning *Orthochirus socotrensis* (Pocock).

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Five new prawn-associated gobies (Teleostei : Gobiidae) of the genus *Amblyeleotris*

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Synopsis

Five new species of prawn-associated gobies belonging to the genus *Amblyeleotris* Bleeker are described: *A. rhyax* from the Philippines and Bismarck Archipelago, *A. callopareia* and *A. macronema* from the Great Barrier Reef, *A. latifasciata* from the Gulf of Thailand and Philippines, and *A. diagonalis* from various localities in the Indian Ocean and Western Pacific.

Introduction

The genus *Amblyeleotris* Bleeker is close to *Cryptocentrus* Ehrenberg and includes approximately twenty species of gobies found in association with alpheid prawns in the Indo-Pacific region (Hoese & Steene, ms.; Polunin & Lubbock, in press).

The purpose of the present study is to provide descriptions of five previously unrecorded species: *Amblyeleotris rhyax* from the Philippines and Bismarck Archipelago, *A. callopareia* and *A. macronema* from the Great Barrier Reef, *A. latifasciata* from the Gulf of Thailand and Philippines, and *A. diagonalis* from various localities in the Indian Ocean and Western Pacific.

Methods of description follow Polunin & Lubbock (1977). Type specimens are deposited at the British Museum (Natural History), London (BMNH), the Australian Museum, Sydney (AMS), the National Museum of Natural History, Washington (USNM), the Muséum d'Histoire Naturelle, Genève (MHNG), and the Bernice P. Bishop Museum, Honolulu (BPBM).

Amblyeleotris rhyax n. sp.

(Fig. 1)

MATERIAL EXAMINED

(a) Holotype, 63·7 mm S.L. (standard length), in sandy gully amongst coral at 35 m depth, Nodup, near Rabaul, New Britain, Bismarck Archipelago, coll. R. Lubbock on 1.8.1975; BMNH 1978.2.28.8.

(b) Paratype, 72·5 mm S.L. (ripe ♀), rubble near cave at 35–45 m depth, Nodup, near Rabaul, New Britain, Bismarck Archipelago, coll. R. Lubbock & B. Parkinson on 29.7.1975; USNM. 218978. (c) Paratype, 70·0 mm S.L., 30° rubble slope at 35 m depth, Maribago, Mactan Island, Cebu Strait, Philippine Islands, coll. R. Lubbock on 6.8.1976; AMS. I.20688–001.

DESCRIPTION. Dorsal fin rays VI+I 12 (last ray divided to base); anal fin rays I 12 (last ray divided to base); pectoral fin rays 19–20; pelvic fin rays I 5. 66–71 rows of scales in lateral series from dorsal angle of branchial opening to base of caudal fin, latter with an additional 3–4 rows basally; 24–27 transverse scale series, counted forwards and upwards from first anal spine to approximately below sixth dorsal spine; 21–24 scales in a zigzag series around narrowest part of caudal peduncle. Gill rakers on lower limb of first arch, including elongate raker at angle, 10 or 11 (all elements counted).

The following measurements are presented as percentages of the S.L. Head length 29·6–32·1, mean 31·2; snout length 6·2–7·7, mean 6·8; orbit diameter 6·3–6·5, mean 6·4; predorsal length 31·7–33·8, mean 32·6; snout to origin of second dorsal fin 53·6–55·4, mean 54·6; snout to origin of anal fin 57·5–63·5, mean 60·5; body depth at pelvic fin origin 18·0–20·1, mean 19·0; body width just behind operculum 13·5–15·8, mean 14·4; least depth of caudal peduncle 10·0–10·4, mean

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10·1; dorsal fin base length 50·1–51·3, mean 50·8; first dorsal spine length 12·7–23·1, mean 18·2; second dorsal spine length 14·1–27·1, mean 20·2; third dorsal spine length 15·6–28·0, mean 22·9; fourth dorsal spine length 15·5–29·0, mean 20·5; anal fin base length 23·7–26·2, mean 25·1; pectoral fin length 23·0–24·7, mean 23·7; pelvic fin length 29·3–32·2, mean 30·9; caudal fin length 31·5–34·2, mean 33·1.

Small elongate fish, head and body moderately compressed. Mouth rather large, gape oblique, jaws nearly equal anteriorly (lower jaw protruding slightly in 70·0 mm S.L. paratype), reaching posteriorly approximately to a vertical through centre or hind margin of pupil; upper lip as broad (vertically at front) as lower. Gill opening extending forwards ventrally to vertically below a point just posterior to hind margin of orbit.

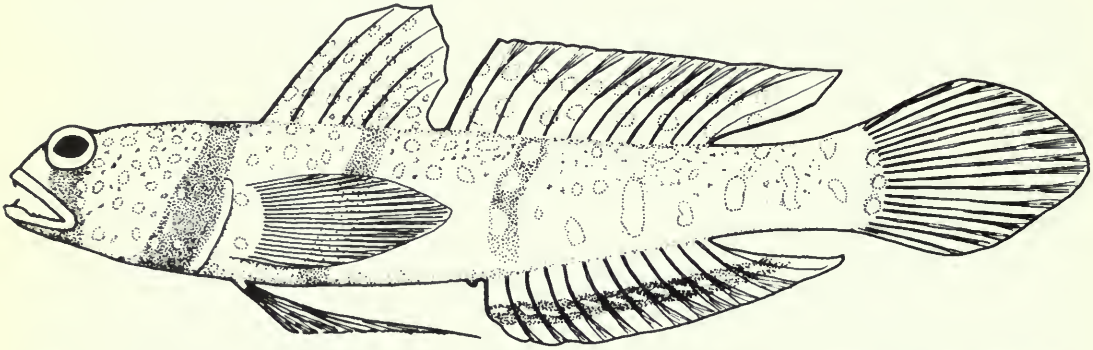

Fig. 1 Diagram showing the live colour pattern of *Amblyeleotris rhyax*, based on the paratype (70·0 mm S.L.) from the Philippine Islands.

Upper jaw with one or two series of fine, sharp, subconical teeth, about three series at symphysis; outer series larger and more caniniform posteriorly, increasingly so anteriorly, with two particularly enlarged teeth anteriorly on each side of jaw. Lower jaw posteriorly with one series of fine, sharp, subconical teeth, about three series at symphysis; outer series larger and more caniniform posteriorly, increasingly so anteriorly with one or two (two on one side in holotype, one in all other cases) greatly enlarged teeth anterolaterally on each side of jaw.

Gill membranes rather narrowly attached at isthmus. Anterior and posterior nostrils separated by a space about equal to width of posterior nostril; posterior nostril oval, about equal in size to round anterior nostril, separated from eye by space about equal to its width; anterior nostril with short membranous tube.

Opercular edge entire, preopercular edge smooth. Scales cycloid anteriorly, becoming ctenoid laterally approximately below hind margin of first dorsal fin. Head almost naked, with a few scales on nape above dorsal angle of branchial opening; midline of nape scaled. Dorsal and anal fins naked; pelvic fins with embedded scales on base; pectoral fins scaled on base; caudal fin with approximately basal seventh scaled.

Sensory papillae on head moderately developed.

Dorsal fin divided into two parts, not connected by membrane; first part with six spines, second, third and fourth spines longest; second part with a single spine followed by branched rays. Anal fin with a single spine followed by branched rays. Origin of anal fin approximately at a vertical below first or second dorsal soft rays. Posterior margins of second dorsal and anal fins pointed. Caudal fin somewhat pointed. Pectoral fins rounded, reaching approximately to anus or to origin of anal fin. Origin of pelvic fins below pectoral fin base; fourth pelvic soft ray longest, reaching to anus or beyond anal fin origin, about three times as long as pelvic spine; fins united by very low membrane, without fraenum.

Colouration. In life, head and body whitish, with four bright red vertical to oblique bands and scattered golden spots; first band from below eye, behind posterior tip of jaw to underside of head; second band across part of predorsal area and hind margin of operculum to underside of head; third band from below fifth to sixth dorsal spines to just behind pelvic fin base; fourth band fainter, from below third to fourth dorsal soft rays to bases of first and second anal rays. First and second vertical bands join a bright red band covering ventral profile of head and body anterior to pelvic fin base. First dorsal fin pale blue with scattered golden spots; second dorsal fin pale blue with golden spots, mostly in two horizontal series. Anal fin pale blue with two horizontal rows of blue spots near base, distally with approximately horizontal golden and dark blue broken lines. Pelvic fins pale blue with a streak of red along inner margin. Pectoral fins hyaline. Caudal fin mainly pale blue, with yellowish tinge along central rays and three to four orange spots at base.

In alcohol, head and body brownish, with bands and spots remaining visible as paler markings. Dorsal, caudal and anal fins pale brown, golden spots becoming hyaline. Pectoral fins hyaline. Pelvic fins brownish.

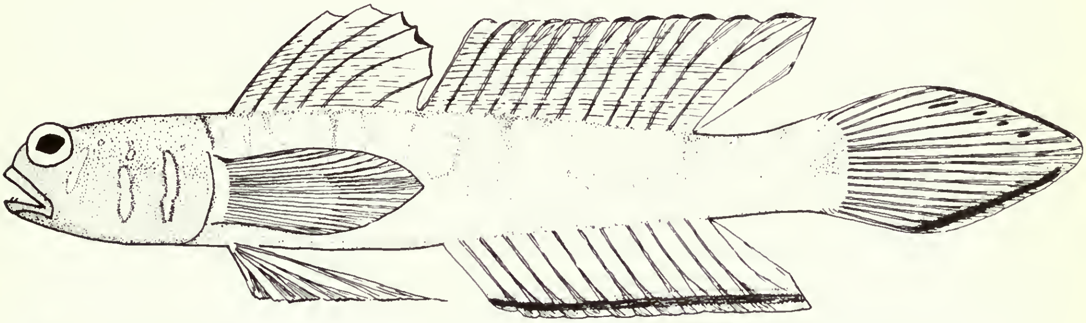

Fig. 2 Diagram showing the live colour pattern of *Amblyeleotris callopareia*, based on the holotype (78·0 mm S.L.) from the Great Barrier Reef.

Remarks. *Amblyeleotris rhyax* most closely resembles *A. guttata* (Fowler, 1938), but the two species can be easily distinguished by live colouration. In *A. rhyax* there are four bright red vertical bands on the head and body (absent in *A. guttata*), and the golden spots on the body do not continue onto the base of the anal fin (as they do in *A. guttata*); furthermore, the area of charcoal grey colouration which covers the ventral part of the body anterior to the anus in *A. guttata* is absent from *A. rhyax*.

The name *rhyax* is derived from ῥυαζ, Greek for volcano, and refers to the fiery colours of the present species.

Habitat and distribution. *Amblyeleotris rhyax* is known from New Britain and the Philippine Islands. It has only been found on outer reef slopes, where it inhabits burrows made by alpheid prawns in sand and rubble at depths usually in excess of 30–40 m.

Amblyeleotris callopareia n. sp.

(Fig. 2)

Material Examined

(a) Holotype, 78·0 mm S.L., at 26 m depth, coarse sand 50–100 m seaward of coral at bottom of reef slope, just east of South Island, Lizard Island, Great Barrier Reef, coll. R. Lubbock on 24.5.1975; BMNH 1978.2.28.1.

(b) Paratype, 68·2 mm S.L., coll. with (a); AMS. I.20689–001.

(c) Paratype, 34·7 mm S.L., coll. with (a); USNM. 218980.

Description. Dorsal fin rays VI + I 12 (last ray divided to base); anal fin rays I 12–13 (last ray divided to base); pectoral fin rays 19–20; pelvic fin rays I 5. 69–75 rows of scales in lateral series from dorsal angle of branchial opening to base of caudal fin, latter with an additional 3–4 rows basally; 21–25 transverse scale series, counted forwards and upwards from first anal spine to approximately below sixth dorsal spine; 19–23 scales in a zigzag series around narrowest part of caudal peduncle. Gill rakers on lower limb of first arch, including elongate raker at angle, 9 or 10 (all elements counted).

The following measurements are presented as percentages of the S.L. Head length 25·8–31·1, mean 28·0; snout length 5·4–6·9, mean 5·9; orbit diameter 5·6–6·9, mean 6·2; predorsal length 31·5–36·3, mean 33·5; snout to origin of second dorsal fin 53·3–57·6, mean 55·3; snout to origin of anal fin 55·2–61·9, mean 59·5; body depth at pelvic fin origin 15·8–18·4, mean 16·8; body width just behind operculum 11·1–13·2, mean 12·3; least depth of caudal peduncle 10·1–10·8, mean 10·4; dorsal fin base length 49·8–54·2, mean 52·5; first dorsal spine length 17·2–18·7, mean 17·8; second dorsal spine length 14·4–20·7, mean 18·3; third dorsal spine length 18·7–21·2, mean 20·2; fourth dorsal spine length 19·3–20·9, mean 20·1; anal fin base length 23·9–30·8, mean 27·6; pectoral fin length 22·4–27·0, mean 24·0; pelvic fin length 26·0–26·8, mean 26·3; caudal fin length 34·7–37·8, mean 35·9.

Small elongate fish, head and body moderately compressed. Mouth rather large, gape oblique, jaws nearly equal anteriorly; upper lip as broad (vertically at front) as lower. Gill opening extending forwards ventrally to vertically below a point approximately one-third of way from hind margin of orbit to posterior margin of operculum.

Upper jaw posteriorly with one or two series of fine, sharp, subconical teeth, about five series at symphysis; outer series larger and more caniniform posteriorly, increasingly so anteriorly, with two particularly enlarged teeth anteriorly on each side of jaw. Lower jaw posteriorly with one or two series of fine, sharp, subconical teeth, about five series at symphysis; outer series larger and more caniniform posteriorly, increasingly so anteriorly, with three particularly enlarged teeth anterolaterally on each side of jaw.

Gill membranes rather narrowly attached at isthmus. Anterior and posterior nostrils separated by a space about twice length of posterior nostril; posterior nostril oval, about 2½ times size of round anterior nostril, separated from eye by space equal to two-thirds of its length; anterior nostril with short membranous tube.

Opercular edge entire, preopercular edge smooth. Scales cycloid anteriorly, becoming ctenoid laterally approximately below sixth dorsal spine. Head largely naked; midline of nape scaled. Dorsal and anal fins naked; pelvic and pectoral fins with scales on base; caudal fin with approximately basal sixth scaled.

Sensory papillae on head moderately developed.

Dorsal fin divided into two parts, not connected by membrane; first part with six spines, second, third and fourth spines longest; second part with a single spine followed by branched rays. Origin of anal fin approximately at a vertical through first or second dorsal soft rays. Posterior margins of second dorsal and anal fins pointed. Caudal fin somewhat pointed. Pectoral fins rounded, reaching approximately to anus. Origin of pelvic fins below pectoral fin base; fourth pelvic soft ray longest, reaching to anus or anal fin origin, about three times as long as pelvic spine; fins united, with fraenum.

Colouration. In life, head and body pale beige with 5 faint vertical to oblique brown bands, and yellow stripes and spots; first band particularly faint, across part of predorsal area above dorsal angle of branchial opening; second band below fifth to sixth dorsal spines; third band below second to fifth dorsal soft rays; fourth band starting from below, and just posterior to, twelfth dorsal soft ray; fifth band on caudal fin base. Irregular scattered spots and patches of brown in between vertical bands. Three more or less vertical golden yellow stripes on head; first stripe from behind centre of hind margin of orbit to half-way down to posterior tip of jaw; second stripe on hind part of preoperculum; third stripe on operculum; a few scattered golden yellow spots above stripes on head; scattered very faint pale yellow spots on body. First dorsal fin very pale beige with very faint horizontal to oblique lines of pale blue and faint orange distal margin, latter most notable between tips of fourth and fifth spines; second dorsal fin similar to first dorsal fin, but with faint dark margin. Anal fin pale greenish beige with black distal margin lined on each side by pale iridescent blue. Pelvic fins pale blue. Pectoral fins hyaline. Caudal fin very pale beige with faint pale blue speckles; ventral margin coloured similarly to distal margin of anal fin; dorsal margin dark, similar to distal margin of second dorsal fin; series of small blue spots posteriorly in upper half of fin, separated from margin by pale bluish band.

In alcohol, head and body pale beige to brown, with brown bands and markings visible as patches of darker brown. Dorsal fins pale beige to hyaline, first dorsal fin with orange margin still visible as black area; bands still visible on anal fin in differing shades of brown; pelvic fins brown; pectoral fins hyaline; caudal fin brown with traces of markings still clearly visible.

Remarks. *Amblyeleotris callopareia* most closely resembles *A. macronema*; the two species can easily be distinguished by lateral (97–103 in *A. macronema*; 69–94 in *A. callopareia*) and transverse (29–32 in *A. macronema*; 21–25 in *A. callopareia*) scale counts, and by colouration (golden markings on side of head present in *A. callopareia*, absent in *A. macronema*).

The Greek καλλοπαρειος means beautiful-cheeked, and refers to the distinctive colouration on the side of the head.

Habitat and distribution. *Amblyeleotris callopareia* is known only from the Great Barrier Reef, Austrialia, where it was collected on sand at the base of the reef slope at a depth of 26 m off Lizard Island. It was in association with burrowing alpheid prawns.

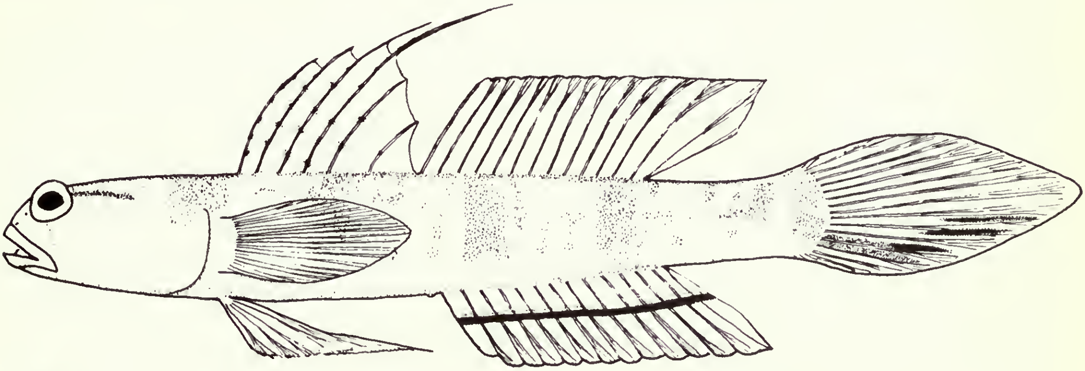

Fig. 3 Diagram showing the live colour pattern of *Amblyeleotris macronema*, based on the holotype (80·0 mm S.L.) from the Great Barrier Reef.

Amblyeleotris macronema n. sp.
(Fig. 3)

Material examined

(a) Holotype, 80·0 mm S.L., at 26 m depth, coarse sand 50–100 m seaward of coral at bottom of reef slope, just east of South Island, Lizard Island, Great Barrier Reef, coll. R. Lubbock on 24.5.1975; BMNH 1978.2.28.5.
(b) Paratype, 77·8 mm S.L., coll. with (a); AMS. I.20689–002.
(c) Paratype, 51·6 mm S.L., coll. with (a); USNM. 218979.
(d) Paratype, 50·0 mm S.L., coll. with (a); MHNG 1592.51.

Description. Dorsal fin rays VI+I 12–13 (last ray divided to base); anal fin rays I 13 (last ray divided to base); pectoral fin rays 16–20; pelvic fin rays I 5. 97–103 rows of scales in lateral series from dorsal angle of branchial opening to base of caudal fin, latter with an additional 4–6 rows basally; 29–32 transverse scale series, counted forwards and upwards from first anal spine to approximately below sixth dorsal spine; 26–27 scales in a zigzag series around narrowest part of caudal peduncle. Gill rakers on lower limb of first arch, including elongate raker at angle, 9 or 10 (all elements counted).

The following measurements are presented as percentages of the S.L. Head length 25·8–29·6, mean 27·8; snout length 5·0–7·4, mean 6·2; orbit diameter 5·8–6·4, mean 6·1; predorsal length 28·7–33·9, mean 31·4; snout to origin of second dorsal fin 51·1–55·6, mean 53·8; snout to origin of anal fin 55·0–57·9, mean 56·8; body depth at origin of pelvic fin 15·0–17·6, mean 16·6; body width just posterior to operculum 10·2–11·2, mean 10·6; least depth of caudal peduncle 9·0–9·8, mean 9·2; dorsal fin base length 52·3–56·0, mean 53·9; first dorsal spine length 14·7–16·4, mean 15·5; second dorsal spine length 18·6–27·2, mean 20·9; third dorsal spine length 30·4–42·8, mean

33·7; fourth dorsal spine length 31·2–39·2, mean 35·0; anal fin base length 27·8–30·2, mean 29·0; pectoral fin length 20·4–22·2, mean 21·4; pelvic fin length 26·0–30·6, mean 27·7; caudal fin length 35·3–41·0, mean 37·4.

Small elongate fish, head and body moderately compressed. Mouth rather large, gape oblique, jaws nearly equal anteriorly (lower jaw protruding slightly in holotype), reaching posteriorly approximately to a vertical through centre of pupil (behind centre of pupil in larger specimens; anterior to centre of pupil in smaller specimens); upper lip as broad (vertically at front) as lower. Gill opening extending forwards ventrally to vertically below a point just posterior to hind margin of orbit.

Upper jaw posteriorly with one or two series of fine, sharp, subconical teeth, about five series at symphysis; outer series slightly larger and more caniniform posteriorly, increasingly so anteriorly, with 2–3 greatly enlarged teeth anteriorly in each side of jaw. Lower jaw posteriorly with one series of fine, sharp, subconical teeth, about four series at symphysis; outer series slightly larger and more caniniform posteriorly, increasingly so anteriorly, with a single particularly enlarged recurved canine anterolaterally on each side of jaw.

Gill membranes rather narrowly attached at isthmus. Anterior and posterior nostrils separated by space about three times width of posterior nostril; posterior nostril round, larger than round anterior nostril, separated from eye by space about equal to twice its width; anterior nostril with short membranous tube.

Opercular edge entire, preopercular edge smooth. Scales cycloid anteriorly, becoming ctenoid laterally between sixth dorsal spine and hind margin of first dorsal fin. Head almost naked, with a few scales on nape above dorsal angle of branchial opening; midline of nape not scaled. Dorsal and anal fins naked; pelvic fins mostly naked, with a few embedded scales on base; pectoral fins mostly naked, with a few embedded scales near ventral margin of base; caudal fin with approximately basal sixth scaled.

Sensory papillae on head moderately developed.

Dorsal fin divided into two parts, not connected by membrane; first part with six spines, third and fourth spines longest; second part with a single spine followed by branched rays. Anal fin with a single spine followed by branched rays. Origin of anal fin approximately at a vertical through second soft dorsal ray. Posterior margins of second dorsal and anal fins somewhat angular. Caudal fin lanceolate. Pectoral fins rounded, reaching about nine-tenths of way to anal fin origin. Origin of pelvic fins below pectoral fin base; fourth pelvic soft ray longest, reaching to just beyond anus or to origin of anal fin, about three times as long as pelvic spine; fins united, with low fraenum over approximately basal fifth of fins.

Colouration. In life, head and body pale beige, with 5 faint brown vertical bands; first band across part of predorsal area, continuing onto dorsal part of operculum; second band below fifth and sixth dorsal spines, fading ventrally; third band below second to fifth dorsal soft rays; fourth band below tenth to twelfth soft dorsal rays; fifth band on caudal fin base. Scattered patches of pale brown between vertical bands. Brown band along midline of ventral profile of head, lined with pale blue; a few pale blue spots on and above preoperculum. First dorsal fin very pale beige with pale blue and orange spots, latter arranged regularly along spines and becoming brighter distally; second dorsal fin very pale beige with a few orange spots along anterior and distal margins. Anal fin pale bluish hyaline distally, pale beige along base, the two colours separated by iridescent pale blue band and broad horizontal black stripe. Pelvic fins pale bluish hyaline. Pectoral fins hyaline. Caudal fin very pale beige, ventral half with dark streaks lined with pale blue, dorsal half with faint orange margin and scattered pale blue spots near upper edge.

In alcohol, head and body pale beige with brown bands and patches still visible. Spots on dorsal fins scarcely visible; black stripe on anal fin remains striking; pelvic and pectoral fins hyaline; black streaks on lower half of caudal fin remain visible

REMARKS. *Amblyeleotris macronema* is close to *A. callopareia*; for a comparison between the two species see 'Remarks' under *A. callopareia.*

The name *macronema* comes from the Greek μακρος (=long) and υημα (=thread), and refers to the long spines of the first dorsal fin.

HABITAT AND DISTRIBUTION. *Amblyeleotris macronema* is known from Lizard Island, Great Barrier Reef, where it was found on coarse sand at the base of the reef slope at a depth of 26 m; it lives in association with burrowing alpheid prawns.

Amblyeleotris diagonalis n. sp.
(Fig. 4)

MATERIAL EXAMINED

(a) Holotype, 37·5 mm S.L., at 25 m depth on coarse sand 10–30 m seaward of coral at bottom of reef slope, just east of South Island, Lizard Island, Great Barrier Reef, coll. R. Lubbock on 23.5.1975; BMNH 1978.2.28.2.

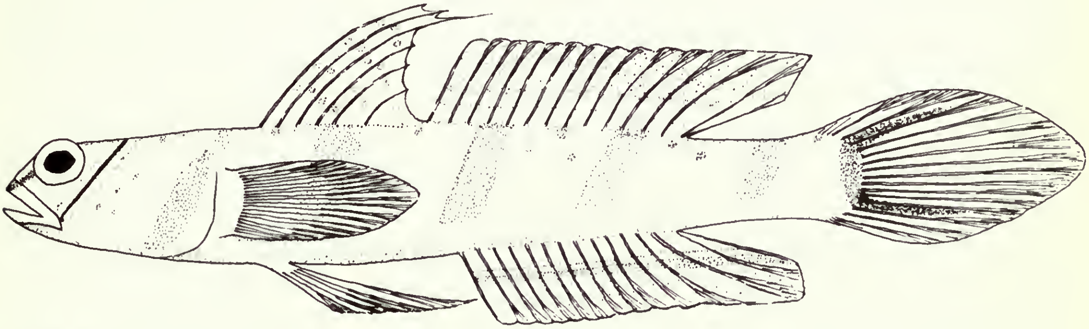

Fig. 4 Diagram showing the live colour pattern of *Amblyeleotris diagonalis*, based on the paratype (59·5 mm S.L.) from the Andaman Sea.

(b) 2 Paratypes, 44·1–51·9 mm S.L., coll. with (a); AMS. I.20690–001.
(c) 2 Paratypes, 45·9–56·0 mm S.L., on sand on reef flat at 6 m depth, southeast side of Nossi Iranja, northwest Madagascar, coll. N. Polunin on 9.7.1973; MHNG 1592.49–50.
(d) Paratype, 39·1 mm S.L., sand adjacent to coral reef at 17 m depth, south side of Tany Kely Island, Nossi Bé, Madagascar, coll. N. Polunin on 30.6.1973; BMNH 1978.2.28.3.
(e) Paratype, 32·0 mm S.L., on sand next to rock at 20 m depth, Lively Rocks, Trincomalee, Sri Lanka, coll. J. E. Randall on 3.4.1975; BPBM 18821.
(f) 2 Paratypes, 36·2–39·7 mm S.L., on rubble and sand at 10 m depth, north side of Fort Frederick Peninsula, Trincomalee, Sri Lanka, coll. J. E. Randall on 3–5.4.1975; BPBM 18821.
(g) Paratype, 59·5 mm S.L., on rubble and sand interspersed with coral at 30 m depth, west point of Born (Perforated) Island, eastern Andaman Sea, coll. N. Polunin & R. Lubbock on 8.3.1977; USNM. 218981.

DESCRIPTION. Dorsal fin rays VI + I 13 (last ray divided to base); anal fin rays I 13 (last ray divided to base); pectoral fin rays 19–20; pelvic fin rays I 5. 67–75 rows of scales in lateral series from dorsal angle of branchial opening to base of caudal fin, latter with an additional 4–5 rows basally; 23–24 transverse scale series, counted forwards and upwards from first anal spine to approximately below sixth dorsal spine; 19–22 scales in a zigzag series around narrowest part of caudal peduncle. Gill rakers on lower limb of first arch, including elongate raker at angle, 8–10 (all elements counted).

The following measurements are presented as percentages of the S.L. Head length 26·7–29.9, mean 27·9; snout length 5·7–6·9, mean 6·4; orbit diameter 6·7–8·2, mean 7·5; predorsal length 32·2–34·4, mean 33·1; snout to origin of second dorsal fin 52·1–54·6, mean 53·5; snout to origin of anal fin 55·9–57·4, mean 56·8; body depth at pelvic fin origin 15·8–19·6, mean 17·3; body width just behind operculum 11·0–12·8, mean 11·7; least depth of caudal peduncle 9·3–10·9, mean 10·2; dorsal fin base length 49·1–55·6, mean 52·4; first dorsal spine length 16·6–29·2, mean 22·6;

second dorsal spine length 17·4–27·7, mean 23·5; third dorsal spine length 16·5–28·0, mean 21·9; fourth dorsal spine length 13·0–20·6, mean 17·0; anal fin base length 27·2–30·0, mean 28·5; pectoral fin length 21·5–26·1, mean 23·9; pelvic fin length 29·4–33·1, mean 30·8; caudal fin length 29·6–42·1, mean 34·6.

Small elongate fish, head and body moderately compressed. Mouth rather large, gape oblique, jaws nearly equal anteriorly, reaching posteriorly approximately to a vertical through centre of pupil; upper lip as broad (vertically at front) as lower. Gill opening extending forwards ventrally to vertically below a point one-quarter of way from hind margin of orbit to posterior edge of preoperculum.

Upper jaw posteriorly with two series of fine, sharp, subconical teeth, about four series at symphysis; outer series larger and more caniniform posteriorly, increasingly so anteriorly, with three to four particularly enlarged teeth anteriorly in each side of jaw. Lower jaw posteriorly with one series of fine, sharp, subconical teeth, about five series at symphysis; outer series generally larger and more caniniform, especially anteriorly, with four particularly enlarged teeth anteriorly in outer series, and three to four particularly enlarged teeth anterolaterally in inner series, in each side of jaw.

Gill membrane rather narrowly attached at isthmus. Anterior and posterior nostrils separated by a space about equal to width of posterior nostril; posterior nostril oval, about equal in size to round anterior nostril, separated from eye by space slightly less than its width; anterior nostril with short membranous tube.

Opercular edge entire, preopercular edge smooth. Scales cycloid anteriorly, becoming ctenoid laterally approximately below origin of dorsal fin. Head almost naked, with a few scales on nape above dorsal angle of branchial opening; midline of nape scaled. Dorsal and anal fins naked; pelvic fins with embedded scales on base; pectoral fins scaled on base; caudal fin with approximately basal fifth scaled.

Sensory papillae on head moderately developed.

Dorsal fin divided into two parts, not connected by membrane; first part with six spines, first, second and third spines longest; second part with a single spine followed by branched rays. Anal fin with single spine followed by branched rays. Origin of anal fin approximately at a vertical below first to second dorsal soft rays. Posterior margins of second dorsal and anal fins pointed. Caudal fin somewhat pointed. Pectoral fins rounded, reaching approximately to just beyond anus. Origin of pelvic fins below pectoral fin base; fourth pelvic soft ray longest, usually marginally longer than fifth, reaching to bases of first to third anal soft rays, about three times as long as pelvic spine; fins united by a very low membrane, without fraenum.

Colouration. In life, head and body whitish, becoming greyish dorsally, with six oblique brown bands; first band narrower and darker than others, from nape to posterior tip of maxilla; second band from predorsal area across operculum; third band from bases of fifth and sixth dorsal spines; fourth band from bases of third and fourth dorsal soft rays; fifth band from bases of tenth to twelfth dorsal soft rays; sixth band on caudal peduncle, anterior to caudal fin base. Pale iridescent blue narrow lines on preoperculum, operculum and nape, mostly adjacent and parallel to first and second oblique brown bands. Traces of brown, mostly spots, dorsally between oblique body bands; thin brown lines from each eye anteriorly to tip of snout. First dorsal fin whitish hyaline, with small red spots margined with pale blue; second dorsal fin yellowish basally with faint blue markings, distal half pale brownish hyaline. Anal fin with light yellowish basal band, separated from greyish hyaline distal half by one blue and one red (distally) line. Pelvic fins whitish with faint blue and red tinges. Pectoral fins hyaline. Caudal fin yellowish with faint pale blue spots, and brown crescent formed by faint brown bar just posterior to base of fin extending ventrally and dorsally towards hind margin of fin.

In alcohol, head and body pale beige, with bands, lines on snout, and spots pale to dark brown. Dorsal, caudal, pectoral and pelvic fins largely hyaline. Anal fin mostly hyaline, with blue and red horizontal lines turning dark brown.

REMARKS. *Amblyeleotris diagonalis* is close to *A. steinitzi* (Klausewitz, 1974) and *A. japonica* Takagi, 1957, but may easily be distinguished by colouration. In *A. diagonalis* there is a conspicuous, narrow, dark brown band from the nape to the posterior tip of the maxilla; this is absent in both *A. steinitzi* and *A. japonica.*

The Latin name *diagonalis* refers to the oblique bands on the body.

HABITAT AND DISTRIBUTION. *Amblyeleotris diagonalis* has a wide distribution, having been collected in Madagascar, Sri Lanka and the Andaman Sea, and also on the Great Barrier Reef. It occurs in sandy habitats, where it lives symbiotically with burrowing alpheid prawns.

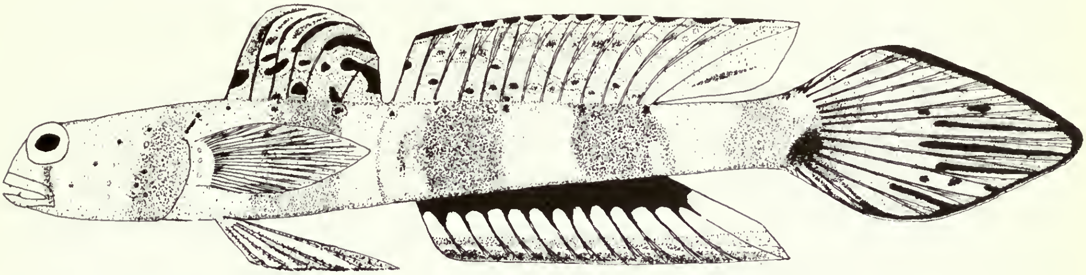

Fig. 5 Diagram showing the live colour pattern of *Amblyeleotris latifasciata*, based on the holotype (65·1 mm S.L.) from the Philippine Islands.

Amblyeleotris latifasciata n. sp.
(Fig. 5)

MATERIAL EXAMINED

(a) Holotype, 65·1 mm S.L., at 15 m depth, on rubble at a distance of 10 m from nearest coral, passage between Cabulan Island and Vandanon Island, Cebu Strait, Philippine Islands, coll. R. Lubbock on 21.8.1976; BMNH 1978.2.28.4.
(b) Paratype, 75·3 mm S.L., on sand and rubble at 10–25 m depth, north side of Chuang Island, off Samae San, Sattahip, Gulf of Thailand, coll. N. Polunin & R. Lubbock on 15.3.1977; AMS. I.20691–001. (c) Paratype, 67·2 mm S.L., coll. with (b); USNM. 218982.

DESCRIPTION. Dorsal fin rays VI+I 13 (last ray divided to base); anal fin rays I 13 (last ray divided to base); pectoral fin rays 20; pelvic fin rays I 5. 87–92 rows of scales in lateral series from dorsal angle of branchial opening to base of caudal fin, latter with an additional 3–5 rows basally; 29–30 transverse scale series, counted forwards and upwards from first anal spine to approximately below sixth dorsal spine; 25 scales in a zigzag series around narrowest part of caudal peduncle. Gill rakers on lower limb of first arch, including elongate raker at angle, 9 or 10 (all elements counted).

The following measurements are presented as percentages of the S.L. Head length 26·7–27·4, mean 27·1; snout length 5·2–5·3, mean 5·2; orbit diameter 6·1–6·2, mean 6·1; predorsal length 30·7–33·4, mean 32·2; snout to origin of second dorsal fin 50·3–53·2, mean 51·8; snout to origin of anal fin 52·8–55·2, mean 54·2; body depth at pelvic fin origin 15·0–16·0, mean 15·4; body width just posterior to operculum 10·5–11·3, mean 10·8; least depth of caudal peduncle 9·0–9·5, mean 9·2; dorsal fin base length 54·7–55·6, mean 55·0; first dorsal spine length 13·0–19·9, mean 16·6; second dorsal spine length 13·6–18·1, mean 16·3; third dorsal spine length 16·2–19·3, mean 17·3; fourth dorsal spine length 15·5–18·0, mean 16·8; anal fin base length 31·8–33·9, mean 32·7; pectoral fin length 19·9–22·7, mean 21·6; pelvic fin length 24·7–26·4, mean 25·4; caudal fin length 36·7–40·1, mean 37·9.

Small elongate fish, head and body moderately compressed. Mouth rather large, gape oblique, jaws nearly equal anteriorly, reaching posteriorly to a vertical through posterior margin of pupil; upper lip as broad (vertically at front) as lower. Gill opening extending forwards ventrally to a point vertically below hind margin, or just posterior to hind margin, of orbit.

Upper jaw posteriorly with two series of fine, sharp, subconical teeth, about five series at symphysis; outer series slightly larger and more caniniform posteriorly, increasingly so anteriorly; low notched ridge on vomer. Lower jaw posteriorly with one or two series of fine, sharp, subconical teeth, about five series at symphysis; outer series slightly larger and more caniniform posteriorly, increasingly so anteriorly, and with a single particularly enlarged caniniform tooth anterolaterally on each side of jaw.

Gill membranes rather narrowly attached at isthmus. Anterior and posterior nostrils separated by space about equal to length of posterior nostril; posterior nostril round to oval, slightly larger than round anterior nostril, separated from eye by space about equal to its length; anterior nostril with short membranous tube.

Opercular edge entire, preopercular edge smooth. Scales cycloid anteriorly, becoming ctenoid laterally approximately below third soft dorsal ray. Head naked; midline of nape not scaled. Dorsal and anal fins naked; pelvic fins mostly naked, a few embedded scales on base; pectoral fins mostly naked, possibly a few scales close to base; caudal fin with approximately basal sixth scaled.

Sensory papillae moderately developed.

Dorsal fin divided into two parts, not connected by membrane; first part with six spines, first, second, third and fourth spines longest; second part with a single spine followed by branched rays. Origin of anal fin at a vertical through base of second dorsal soft ray. Posterior margins of second dorsal and anal fins angular. Caudal fin rather pointed. Pectoral fins rounded, reaching about nine-tenths of way to anal fin origin. Origin of pelvic fins below pectoral fin base; third and fourth pelvic soft rays longest (approximately equal in length in holotype, fourth ray longest in both paratypes), reaching to or beyond anal fin origin, about four times as long as pelvic spine; fins united, with low fraenum over approximately basal fifth of fins.

Colouration. In life, head and body pale grey to brownish, with 5 copper-coloured broad vertical bands and with scattered pale blue and orange spots; first band across part of predorsal area and hind margin of operculum; second band from below fourth to sixth dorsal spines to just behind pelvic fin base; third band from below second to fifth dorsal soft rays to bases of first to fourth anal soft rays; fourth band from below ninth to twelfth dorsal soft rays to bases of ninth to twelfth anal soft rays; fifth band on caudal peduncle. Pale blue spots mainly on preoperculum, operculum, and along dorsal profile of head and body; orange spots mainly on operculum, nape, and anterior part of body between first and second, and second and third vertical bands. First dorsal fin pale brownish with red spots edged with pale blue; second dorsal fin pale brownish with broken horizontal pale blue lines and with two rows of orange spots, upper row along distal margin of fin, lower row near base of fin; one bright red spot between penultimate and ultimate dorsal fin rays. Anal fin with brown base, separated from a horizontal submarginal red stripe by a band of pale blue; distal margin brownish, lined interiorly with pale blue. Pelvic fins brownish with streaks of pale blue. Pectoral fins hyaline. Caudal fin pale brownish, darker basally, with bright red margin lined interiorly with pale blue dorsally and exteriorly with pale blue ventrally; up to about ten bright red spots edged with light blue, some of spots merging with red margin.

In alcohol, head and body pale brown with bands largely discernible as areas of darker brown; orange and blue spots remain visible as pale spots, the former ringed with darker brown. Fins brownish with markings usually visible as paler areas.

REMARKS. *Amblyeleotris latifasciata* is close to *A. aurora* (Polunin & Lubbock, 1977) and *A. sungami* (Klausewitz, 1969). It can be distinguished from *A. aurora* by the number of soft anal rays (13 in *A. latifasciata*; 14 in *A. aurora*), by certain morphometric characters (head length 26·7–27·4% of S.L. in *A. latifasciata*, 23·2–26·5% in *A. aurora*; length of third dorsal spine 16·2–19·3% of S.L. in *A. latifasciata*, 10·0–16·9% in *A. aurora*; length of caudal fin 36·7–40·1% of S.L. in *A. latifasciata*, 27·4–34·5% in *A. aurora*), and by colouration, notably the colour of the body bands (coppery brown in *A. latifasciata*, pink in *A. aurora*). *A. latifasciata* is readily distinguishable from *A. sungami* by the lateral scale count (87–92 in *A. latifasciata;* 102–108 in *A. sungami*) and by details of colouration; amongst the latter are to be noted the width of the body bands (broad in *A. latifasciata;* narrow in *A. sungami*), and the absence of an elaborate colour pattern on the caudal fin of *A. sungami* (present in *A. latifasciata*). *A. sungami* is only known from the Red Sea, *A. aurora* from the Indian Ocean and *A. latifasciata* from the western Pacific Ocean.

The Latin name *latifasciata* is derived from the words *latus* (=broad) and *fasciatus* (=banded) and refers to the breadth of the bands on the body, which serve to distinguish this species from many related forms.

HABITAT AND DISTRIBUTION. *Amblyeleotris latifasciata* is known from the Gulf of Thailand and the Philippine Islands, where it was collected on sand and rubble at depths of 10–25 m; it lives in symbiosis with burrowing alpheid prawns.

Acknowledgements

For much advice on goby taxonomy we thank D. F. Hoese of the Australian Museum, Sydney. R. L. thanks Gray Cutlack and Brian Parkinson for help with fieldwork in Rabaul, and Johnny Kiener for help in Cebu. N. V. C. P. once more expresses gratitude to Nigel and Gwen Cornfield for facilities on the yacht *Marimba*. We are both grateful to Jeff Farrell, Jerry Welch and Adrian Lamb, who all contributed greatly to the success of our collecting trip in Thailand. We thank P. J. P. Whitehead of the British Museum (Natural History) for reviewing the manuscript.

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—— —— (in press). Notes on the gobies (Teleostei : Gobiidae) *Amblyeleotris periophthalmus* and *Amblyeleotris fasciata*. *Rev. fr. Aquariol.*

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The taxonomy of *Procavia capensis* in Ethiopia, with special reference to the aberrant tusks of *P. c. capillosa* Brauer (Mammalia, Hyracoidea)

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Synopsis

Procavia capensis capillosa from the Mendebo Mountains, Bale Province, Ethiopia is redescribed, drawing attention to the peculiar shape of the upper and lower incisors which are unique amongst the Hyracoidea. The characters and distribution of all the subspecies of *P. capensis* in Ethiopia are reviewed and the classification of the genus discussed.

Introduction

Each of the two genera of rock hyraxes, *Procavia* and *Heterohyrax* (s.s.), comprises a series of apparently allopatric forms covering a large part of Africa and, in the case of *Procavia*, the Arabian Region. Both groups are notorious for the great amount of geographical variation, often of a very local nature and no doubt correlated with the high degree of isolation of suitable rocky habitats. Although many forms have been described, no satisfactory comprehensive classification exists for either group. Recent reviews are by Bothma (1971) and Roche (1972).

Several *Procavia* collected in 1972 at high altitude in the Mendebo Mountains, western Bale Province, Ethiopia by Dr D. W. Yalden, Dr P. A. Morris and Dr M. J. Largen appear referable to *P. capensis capillosa* Brauer, 1917 but show peculiarities of the upper and lower incisors that set them apart from all other known specimens of *Procavia* and indeed of Hyracoidea. These features were not, however, mentioned in the original description of *capillosa*, which was based on a single female, and appear never to have been described.

The upper tusks of normal male hyracoids are unparalleled in shape in any other mammals and are remarkably constant throughout all three extant genera. The following numbers of male specimens with permanent upper incisors have been examined without finding any deviation from the norm comparable to that seen in the specimens of *capillosa: Procavia* – 157, *Heterohyrax* s.s. – 80, *Dendrohyrax* – 89. The incisors of female *P. c. capillosa* are also distinctive but less so than those of the males.

Bothma (1971) recognized five species of *Procavia* but these have not been satisfactorily defined and I am inclined to accept the view of Roche (1972) that all should be considered conspecific. The variation thus included within one species is, however, rather extreme and much remains to be done before it is adequately described. Although the character of the tusks sets *capillosa* apart from all other hyracoids, it seems unlikely that it would give rise to reproductive isolation and I therefore propose that subspecific rank is appropriate.

Redescription of *Procavia capensis capillosa*

Procavia erlangeri capillosa Brauer, 1917. Type locality Adaba (=Agada), 7°00′ N, 39°24′ E, western Bale Province, Ethiopia. Holotype: Zoologisches Museum, Berlin no. 21759, skin and skull (latter originally no. 21760) of an adult female, labelled 'Agada, 8.II.01, Dr Ellenbeck'. The locality was given by Brauer as 'Agada am Abunass und Semaeno im Arussi Lande' but only one specimen was detailed. The route map in Erlanger (1904) shows 'Adaba (Agada)' at the locality shown on modern maps as Adaba. The type locality can therefore be restricted as

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above. Abunass probably refers to the locality of that name much further east at about 7°25′ N, 40°25′ E but there is no evidence that *capillosa* as here understood occurs there.

SPECIMENS EXAMINED. The holotype skull; also the following, all from the Mendebo (Bale) Mountains, near Dinshu (=Gurie), 7°06′ N, 39°47′ E and up to 20 km westwards ('Shifta Rock' between Dinshu and Adaba), at altitudes from 3100 to 3500 m. All but the first two were found as skulls and therefore were not sexed other than by the tusks.

BMNH 1972.1078	♂	ad.	skull, skin	M^3 erupted, moderately worn
BMNH 1972.1079	♂	ad.	skull, skin	M^3 erupted, moderately worn
BMNH 1972.1080	?	ad.	skull only	M^3 erupted, no mandibles, no incisors
BMNH 1972.1081	?	ad.	skull only	M_3 erupted, mandibles only
BMNH 1972.1082	[♀]	subad.	skull only	M^2 erupted, complete
BMNH 1972.1083	?	ad.	skull only	M^3 erupted, no incisors
BMNH 1972.1084	?	juv.	skull only	P^{1-4} only, no upper incisors
BMNH 1972.1077	[♀]	ad.	skull only	M^3 erupting, no mandibles
BMNH 1976.121	[♀]	ad.	skull only	M^3 erupting, no mandibles
BMNH 1976.122	?	juv.	skull only	P^{1-3} only

DIAGNOSIS. Pelage long and dense; dorsal flash black; upper incisors of males and females convergent, with flat anterior surfaces; lower incisors parallel; P_1 generally absent in adults; P^1 generally present and double-rooted.

DESCRIPTION. Pelage long, dense and soft, containing many fine, wavy wool fibres (seen elsewhere in the genus only in *P. capensis mackinderi* from comparable altitudes on Mount Kenya). Dorsal pelage creamy brown with dark grey hair-bases showing, giving an irregular mottled appearance (as in *P.c. erlangeri* but much less orange) rather than a neat agouti effect. Grey bases concealed more effectively on nape, giving pale collar. Head darker than back, especially on cheeks and around eyes, but much less dark than in *P. c. erlangeri*. Hairs around dorsal gland black, much more prominent than in *P. c. erlangeri* but rather less prominent than in *P. c. scioana*. Slight yellow spot on hind margin of black patch. Naked glandular area about 15–20 mm wide and 30–35 mm long. Ventral pelage creamy buff, much less orange than in *P. c. erlangeri*, similar to *P. c. scioana* and many other forms. Feet similar in colour to back. Vibrissae black, distributed as in other *Procavia*.

Skull differing from that of other *Procavia* in the following features (Fig. 1): upper incisors of adult males convergent, with flat anterior surfaces; of adult female similar but smaller and less angular, although much flatter and wider than in females of other subspecies; lower incisors parallel in both sexes. The two adult male skulls also lack any ridge or overhanging crest on the maxilla below the anteroventral margin of the orbit (a condition normal in females elsewhere but rare in adult males). A three-pronged pectination of the lower incisors is visible on all four teeth of the presumed female with M^2 erupted (1972.1082) but not on the much more worn teeth of the fully adult males.

P^1 is lacking on both sides in one of the adult males (slightly the older judging by tooth-wear and cranial crests) but present and double-rooted in the other and in the four other fully adult skulls. In the subadult female it is present only on the left. P_1 is lacking in all six adult or subadult mandibles, although single alveoli are present in one (M_3 erupted).

In the holotype, a presumed female, the upper incisors are less convergent than in the others, leaving a gap of 2 mm between the tips, but they are nevertheless quite different in shape from those of either sex of other races.

MEASUREMENTS (Table 1). Similar in size to other large forms of *P. capensis*, e.g. *P. c. scioana* and *P. c. erlangeri*.

Measurements of the only adult animal measured in the flesh (BMNH 1972.1079, ♂, M^3 moderately worn): head and body 555 mm; hind feet 75 mm; ear 35 mm; weight 4·25 kg.

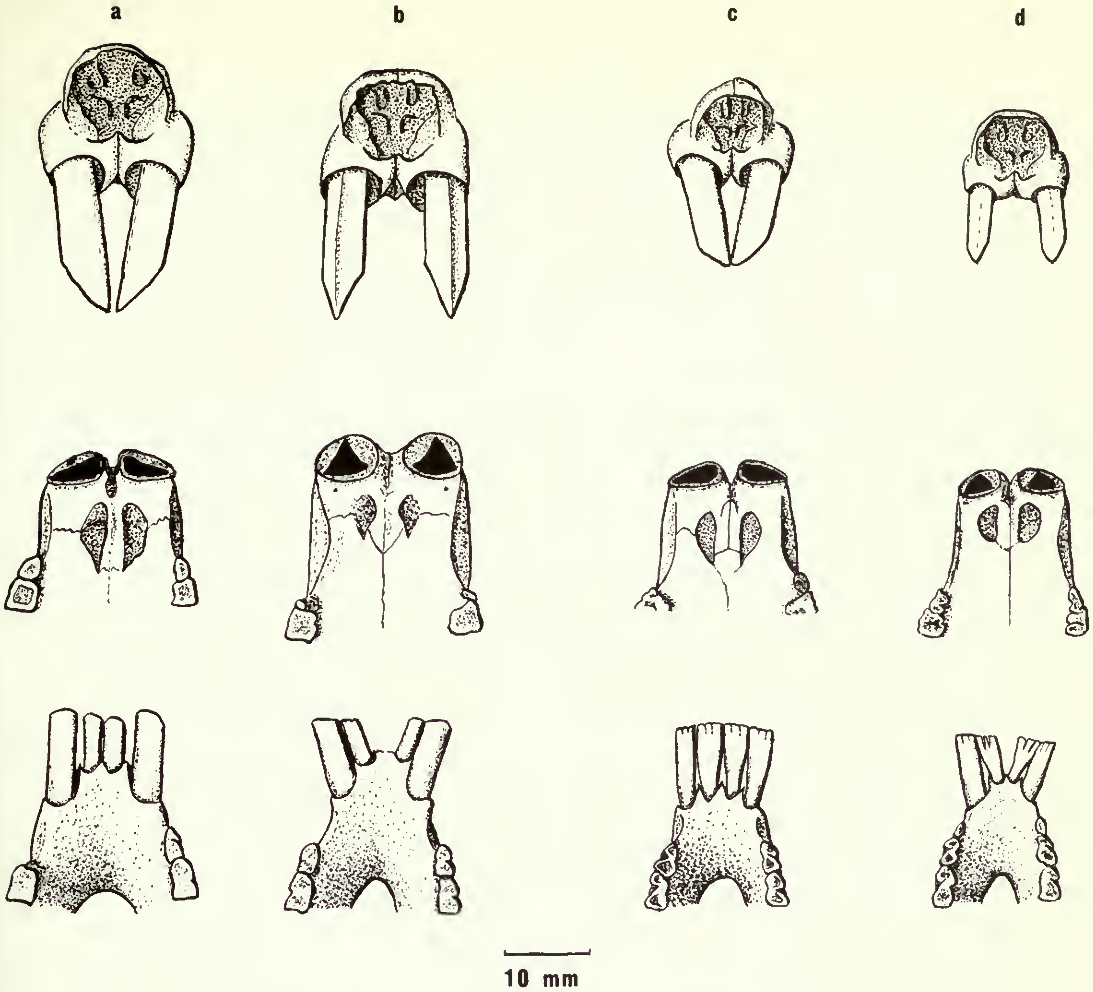

Fig. 1 Incisors of *Procavia capensis* from Ethiopia.
Top: anterior view of upper incisors; centre: ventral view showing, in black, the upper incisors as they would appear in transverse section at the alveoli; bottom: dorsal view of lower incisors.
(a) *P. c. capillosa*, Bale Prov., adult ♂ (M^3 worn), BMNH 1972.1079; (b) *P. c. erlangeri*, Dire Dawa, Harar Prov., adult ♂ (M^3 worn), BMNH 34.11.20.8; (c) *P. c. capillosa*, Bale Prov., subadult ♀ (M^2 erupted), BMNH 1972.1082; (d) *P. c. erlangeri*, Dire Dawa, Harar Prov., subadult ♀ (M^2 erupted), BMNH 34.11.20.6.

HABITAT. Rocky outcrops between 3100 and 3500 m in *Erica arborea* and *Juniperus* zones much degraded by heavy grazing to a mosaic of grass and scrub (D. Yalden, in litt.).

Variation of *Procavia* in Ethiopia

The localities shown on the map (Fig. 2) represent the specimens of *Procavia* from Ethiopia in the collection of the British Museum (Natural History) that are sufficiently localized, along with the few others that have been seen or that have been reported in the literature in sufficient detail. A general distinction can be made between the high altitude forms, which are variable but large, dark and with a black or obscure dorsal flash, and the forms in the surrounding lowland savanna and steppe zones. These latter appear much more uniform than is suggested by the existing litera-

Table 1 Characteristics of the principal forms of *Procavia capensis* in Ethiopia.

	habessinica	*scioana*	*capillosa*	*erlangeri*	*jacksoni*
No. of ad. skins examined	14	25	2	10	2
Dorsal flash	Yellow and black, obscure	Black, large	Black, moderately large	Black, obscure	Yellow, large
Dorsal pelage	Dark, greyish brown, rather uniform	Dark, faintly speckled	Greyish brown, mottled	Orange brown, mottled	Brown, speckled (agouti)
Head	Slightly darker than back	Slightly darker than back	Darker than back	Dark, almost black	Slightly darker than back
Woolly underfur	0	0	+	0	0
Feet (upper surface, cf. back)	Same	Paler	Same	Darker	Same
Size (ads with M^3)					
Head and body (mm)	*c.* 450	*c.* 500	555 (1)	465, 510 (2)	535 (1)
Condylobasal length (mm)	80–91 (10)	89–102 (6)	94–99 (5)	87–97 (4)	(87–M^2 only)
P^1–M^3 (mm)	35–40 (12)	37–42 (9)	39–45 (6)	39–42 (5)	–

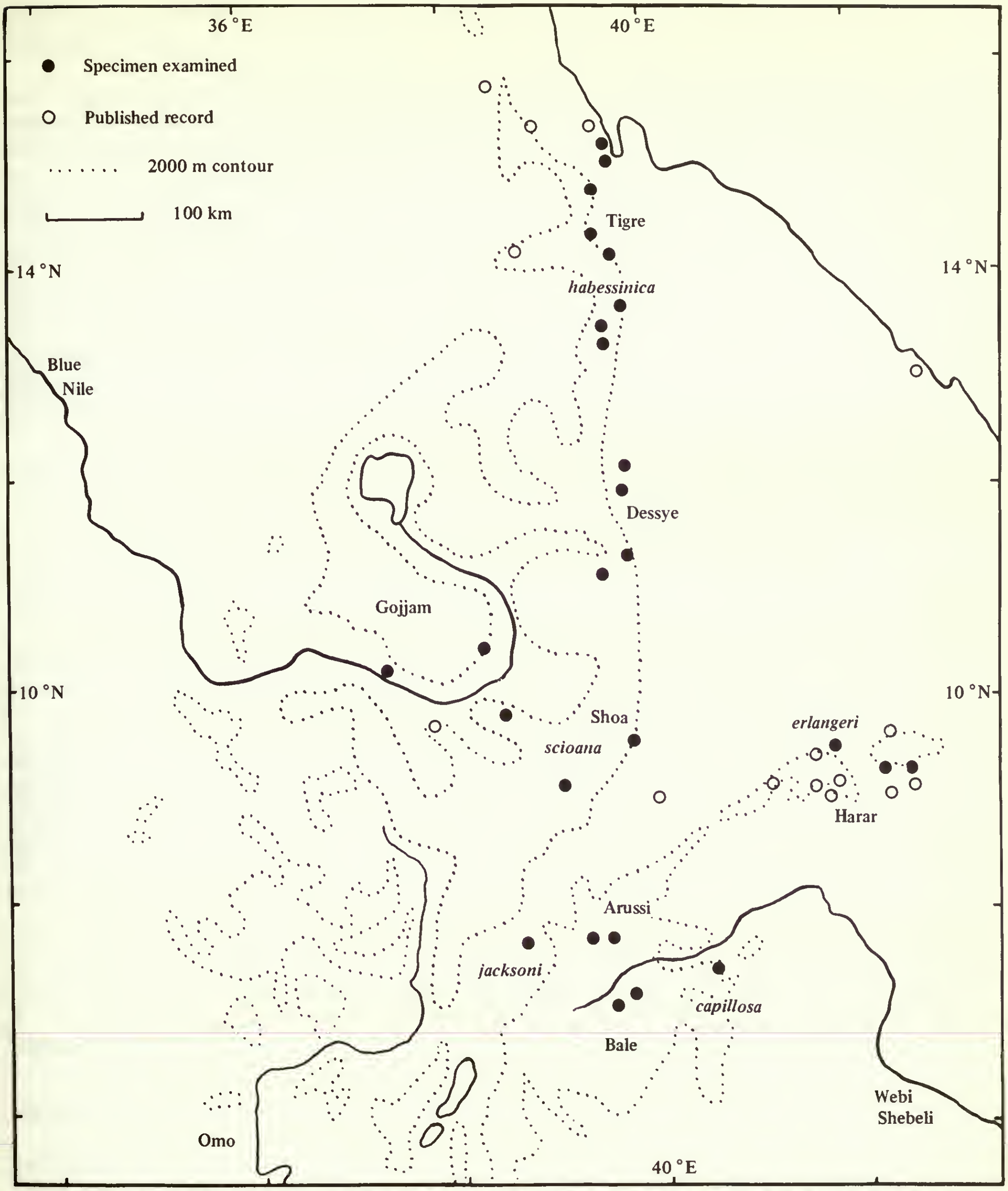
36 °E
40 °E
● Specimen examined
○ Published record
. . . . 2000 m contour
100 km
14 °N
14 °N
Tigre
habessinica
Blue Nile
Dessye
Gojjam
10 °N
10 °N
Shoa
scioana
erlangeri
Harar
Arussi
jacksoni
capillosa
Bale
Webi Shebeli
Omo
40 °E

Fig. 2 The Ethiopian Highlands showing localities from which *Procavia* has been recorded.

ture. A 'typical savanna' form can be recognized ranging from northern Tanzania (*matschiei* Neumann, 1900) through Kenya and Uganda, and across the savanna zone to Senegal, characterized especially by agouti pelage and large yellow dorsal flash. Unfortunately the older names that might apply to this form all relate to divergent peripheral populations – *pallida* Thomas, 1891 (Somalia), *latastei* Thomas, 1892 (Senegal), *kerstingi* Matschie, 1899 (Dahomey). This form penetrates Ethiopia from the south along the Rift Valley (specimens in BM(NH) from Lake Langano) where it can provisionally be called *P. c. jacksoni* Thomas, 1900; it probably also occurs in the southeast (Ogaden) in the form of the very small *P. c. pallida* Thomas, 1891; and probably extends from the west up the Blue Nile where it may be represented by *P. c. meneliki* Neumann, 1902.

In the north, the steppe/desert form resembles the savanna form except that the pelage is more uniformly yellow-brown without marked agouti speckling, the head is not noticeably darker than the back and the dorsal flash, although yellow, is less conspicuous and contrasting. This form extends from Sudan north to Sinai and Lebanon and can be called *P. c. syriaca* with *ruficeps* as a synonym – there is no case for using the name *ruficeps* (type-locality Dongola in northern Sudan) for the more southern savanna form as is so often done, e.g. by Bothma (1971) and Roche (1972). This form probably occurs in northern Ethiopia and may intergrade with the northern highland form *habessinica*. In the south, on the other hand, it seems likely that the high altitude forms are more isolated from the savanna forms by forest, although any such isolation may well be breaking down with the destruction of forest.

The characters of the four highland subspecies that can be recognized are summarized in Table 1, along with those of *P. c. jacksoni* representing the savanna form. These subspecies are briefly reviewed below together with intermediate populations from possibly isolated segments of the plateau.

Highland forms

P. c. habessinica (Hemprich & Ehrenberg, 1828)

TYPE LOCALITY. Arkiko, near Massawa, N.E. Ethiopia.

SYNONYMS. *Euhyrax abyssinicus* Gray, 1868; *Hyrax alpini* Gray, 1868; *Hyrax ferruginea* Gray, 1869; *Hyrax irroratus* var. *luteogaster* Gray, 1869 (all from 'Abyssinia'); *Procavia abyssinica minor* Thomas, 1892, Alali, Red Sea Coast, 13° N.

REMARKS. This form can be recognized along the mountain chain between Massawa on the coast and the region of Quiho and Antalo (13°20′ N) at altitudes up to 2500 m. The presence in the dorsal flash of some hairs with extensive yellow tips makes it somewhat intermediate between *scioana* of the central highlands and *syriaca* in eastern Sudan, but the overall dark colour and dark head are in clear contrast with the uniform yellowish brown of *syriaca* (= *burtoni*). To the south, specimens from the Dessye region are intermediate in size and in the prominence of the black dorsal flash between *habessinica* and the larger *P. c. scioana*.

P. c. scioana (Giglioli, 1888)

TYPE LOCALITY. Ankober, Shoa, central Ethiopia.

SYNONYMS. *Procavia shoana* Thomas, 1892; ? *Procavia butleri* Wroughton, 1911, Jebel Fazogli, Blue Nile, Ethiopia/Sudan border.

REMARKS. Found in the mountains of Shoa, around 3000 m, possibly forming a cline with the smaller *P. c. habessinica* to the north.

The few specimens seen from Gojjam, i.e. northwest of the Blue Nile Gorge, are similar but smaller (condylobasal length of five adults 83–89 mm) and one of the eight skins has the dorsal flash brown rather than black. The form *butleri* has the dorsal flash black but indistinct and can be considered a peripheral highland form.

Specimens from the Arussi Mountains, i.e. southeast of the Rift Valley but north of the Webi Shebeli, appear in some respects intermediate between *P. c. scioana* and *P. c. capillosa*. They are large (condylobasal length of the three adults measured 103, 105 and 109 mm, P^1–M^3 44, 45, 45 mm) and have the dorsal flash black but less prominent. One adult male (Field Museum 27090) has the upper incisors like those of *capillosa* in section although rather thicker, and parallel as in normal *Procavia*. Another adult male from the same locality, Tichu (*c.* 7°45′ N, 39°30′ E), has the tusks normal in every respect.

P. c. capillosa Brauer, 1917

TYPE LOCALITY. Adaba, Mendebo Mts.

REMARKS. This form may be isolated from that in the Arussi Mts to the north by the Webi Shebeli and is probably confined to the mountains of Bale Province.

P. c. erlangeri Neumann, 1901

TYPE LOCALITY. Upper Webi Shebeli, especially around Harar, Ethiopia.

SYNONYM. *Procavia erlangeri comata* Brauer, 1917, Gara Mulata Mts, west of Harar.

REMARKS. The original description agrees well with specimens in the British Museum (Natural History) from around Harar. The black head, yellowish colour and virtual absence of a dorsal flash make this a very distinctive form. The form *comata* was distinguished only by the greater length of the pelage, and can be considered consubspecific. Ingersol (1968) commented on the uniformity of specimens from a wide range of habitats in the Harar area.

Lowland forms

P. c. pallida Thomas, 1891

TYPE LOCALITY. Hekebo Plateau, N. Somalia.

REMARKS. A small form – condylobasal length of an adult female with M^3 worn 73·8 mm, P^1–M^3 31·0 mm. The agouti pelage and yellow dorsal flash relate it to the savanna form.

P. c. jacksoni Thomas, 1900

TYPE LOCALITY. Ravine Station, Kenya.

REMARKS. The sole fully adult specimen from the southern Rift Valley of Ethiopia (Lake Langano) has the dorsal flash prominent and yellow. The crown is slightly rufous, contrasting with the paler yellowish brown back with agouti speckling. This specimen was incorrectly called *P. habessinica alpini* by Corbet & Yalden (1972). Specimens of *jacksoni* in Kenya are rather darker and have the dorsal flash less prominent although comprising wholly yellow hairs.

P. c. syriaca (Hemprich & Ehrenberg, 1828)

TYPE LOCALITY. Mount Sinai.

SYNONYMS. *Hyrax ruficeps* Hemprich & Ehrenberg, 1832, Dongola, N. Sudan; *Hyrax burtoni* Gray, 1868, Egypt.

REMARKS. This form occurs from the northern extremity of the range of the genus, in Lebanon, through Egypt and the Sudan, merging with the savanna form in southern Sudan (specimens from around Khartoum are intermediate), and possibly with *P. c. habessinica* in the hills of extreme northern Ethiopia and eastern Sudan. Setzer (1956) postulated that two species were sympatric in northeastern Sudan, calling them *P. habessinica burtoni* and *P. ruficeps ruficeps* but this appears to have been based on the variable allocation of old specimens from Dongola on the Nile – there has never been a clear demonstration of sympatry of any two forms of *Procavia* at one locality.

Variation of *Procavia* throughout its range

A more superficial examination of specimens from the entire range of the genus suggests the following major groups, some of them with considerably modified local or peripheral variants.

capensis – southern Africa; dorsal flash black; dorsal pelage finely speckled, head usually no darker than back; P_1 usually absent but present at the northeastern extremity (*johnstoni*, Malawi).

welwitschi – Angola/Namibia; dorsal flash yellow, P_1 usually absent.

syriaca – savanna zone from northern Tanzania to Somalia and Senegal, and north through Sudan to Egypt, Sinai, Lebanon and Arabia; dorsal flash yellow, usually clearly defined; dorsal pelage agouti in savanna zone with head darker; more uniform yellowish brown north of Khartoum with head no darker than back; P_1 usually present. Moderately differentiated forms occur on the periphery: Mt Nimba, Mauritania, Hoggar, Jebel Marra, Mt Kenya, Somalia, Arabia.

habessinica – Ethiopian plateau; dorsal flash black or obscure; not strongly agouti, head often dark; P_1 variable; many local variations, some very close to *capensis* s.s.

It is tempting to recognize these as discrete species but they are very difficult to diagnose. In the north the *syriaca* group appears to intergrade with the *habessinica* group in northern and perhaps western Ethiopia. There is a wide gap, from northern Tanzania to southern Malawi, apparently without *Procavia.* The widespread *capensis* s.s in southern Africa is scarcely distinguishable from some members of the *habessinica* group, especially *scioana* from which it differs only in the usual absence of P_1. The southwestern *welwitschi* seems discretely separable from the adjacent *capensis* but is only separable from some of the *syriaca* group by the absence of P_1 which is not constant (Roche, 1972).

The principal difference between this and previous classifications is the separation of *matschiei* (northern Tanzania) and other east African forms with the dorsal flash yellow from *johnstoni* (southern Malawi, dorsal flash black) which is here seen as a peripheral relative of the southern *capensis* s.s. In spite of the great difference in external appearance and wide geographical separation these were considered conspecific (in a split classification) by Hahn (1934), followed by many other authors, mainly on the basis of well-developed P_1.

Heterohyrax in Ethiopia

Heterohyrax brucei occurs throughout most of Ethiopia, sometimes occupying the same rock outcrops as *Procavia*, and their separation in the field can be difficult. The most useful characteristics for recognizing *Heterohyrax* are: dorsal pelage short, neat, agouti; dorsal flash small, discrete, pale cream to rust-orange, hairs concolorous to roots; head scarcely darker than back; discrete pale streak above eye (*Procavia* sometimes has a more diffuse pale zone surrounding the eye or above and behind the eye); ventral pelage grey, less yellowish than in *Procavia.* Size is never so great as in the large forms of *Procavia* (rarely over 480 mm head and body) but colonies of one species show a great range of sizes at any one time due to slow attainment of full adult size. In the hand the clearest external distinction in adult males is the anterior position of the penis in *Heterohyrax* – about 60–70 mm in front of the anus compared with 20–30 mm in *Procavia.*

Immature skulls can be difficult to distinguish but adult skulls of *Heterohyrax* have the teeth rather uniform in size, with the combined length of M^1–M^3 shorter than P^1–P^4 whereas in *Procavia* M^1–M^3 are conspicuously large and together considerably larger than P^1–P^4.

Summary

1. *Procavia capensis capillosa* from the Mendebo Mts, Bale Province, Ethiopia is distinguishable from *P. c. scioana* to the north and *P. c. erlangeri* to the northeast by its woolly pelage and from these and all other hyracoids by the formation of the incisors – uppers convergent, with flat anterior surfaces in both sexes, lowers parallel (consistent, allowing for sexual dimorphism, amongst all seven specimens).

2. The forms *erlangeri*, *capillosa*, *scioana* and *habessinica* form a distinctive, although variable, group in the Ethiopian Highlands with the last showing characters approaching the adjacent lowland *P. c. syriaca.*

3. Four main regional groups are recognized in *P. capensis*, distinguished by overall colour of the dorsal pelage and especially of the 'dorsal flash' around the mid-dorsal gland: *capensis* s.s. and *welwitschi* in southern Africa, *syriaca* in the northern savanna and arid zones and *habessinica* in the Ethiopian highlands.

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Richard Peter Vari

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Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea)

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Synopsis

Various osteological and soft anatomical systems in the families Citharinidae and Distichodontidae were examined to test: the hypothesized monophyly of the unit formed by citharinids and distichodontids

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within characoids; the interrelationships of the nominal genera within these families; and the monophyly of the nominal genera and suprageneric taxa.

The evidence of this study is congruent with the hypothesis that citharinids and distichodontids form a monophyletic subunit of characoids definable by a series of derived characters. However, the arrived at hypothesis of generic interrelationships necessitates several modifications of the previous generic and suprageneric taxonomy of these families. The retention of the previously recognized family Ichthyboridae was found to result in a non-monophyletic family Distichodontidae. Consequently, the Ichthyboridae of earlier workers is sunk into the Distichodontidae. At the generic level, *Congocharax* and *Dundocharax* are placed into synonymy of *Neolebias*, and *Gavialocharax* and *Phagoborus* are synonymized into *Ichthyborus*. These changes resolve the previously non-monophyletic natures of *Neolebias* and *Phagoborus* respectively. The conclusions of this study contraindicate the monophyly of the genus *Distichodus* as presently defined, and cast doubt on the monophyletic nature of *Hemigrammocharax* and *Nannocharax*. These three genera are, nonetheless, tentatively retained until such time as an analysis of the phylogeny of their contained species can be undertaken.

Finally, information uncovered during this study supports the concept of the monophyletic nature of the subunit of characoids formed by the African Characidae. However, the available evidence also indicates that as presently constituted the genus *Alestes* is non-monophyletic. This taxon is, however, retained until an indepth analysis of African characids permits its redefinition on the basis of derived characters. The subdivision of the African Characidae into the subfamilies Hydrocyninae and Alestiinae results in the latter taxon being non-monophyletic. Consequently the Hydrocyninae is sunk into the Alestiinae, which in this broader sense now constitutes a monophyletic unit.

Introduction

The superfamily Characoidea (Rosen & Greenwood, 1970) is one of the largest groups in the ichthyofauna of the Neotropical region and Africa, and one of the major freshwater fish assemblages. Although the classification of the superfamily has undergone extensive revision during the last century, questions on the interrelationships of characoids at all taxonomic levels remain largely unresolved. This paper deals with the relationships between and to a lesser extent within the genera which constitute the African endemic characoid families Citharinidae and Distichodontidae.

A series of workers including Boulenger (1909), Regan (1911) and Gregory & Conrad (1938) have suggested that citharinids and distichodontids form a closely related subunit of characoids, with Regan (1911, p. 22) terming them 'a very natural group of African Fish'. Although Greenwood *et al.* (1966) did not deal with interfamilial relationships within the Characoidea, they do list these families sequentially, a procedure meant to indicate close relationship (Weitzman, pers. commun., in Roberts, 1969, p. 399). Despite this broad consensus, the basis for the hypothesized close relationship of these families has remained obscure. Furthermore, as shown in Table 1 the number and limits of the suprageneric taxa recognized within the families Citharinidae and Distichodontidae have been subject to considerable differences of opinion. The conflicting nature of these classifications is reflected in the history of the group recognized as the subfamily Distichodontinae by Boulenger (1909) and more recently as the family Distichodontidae by Greenwood *et al.* (1966) (both of these concepts differ from the Distichodontidae of this work, see p. 265). This assemblage was subdivided into two subfamilies with different limits by Eigenmann (1909) and Regan (1911). Subsequently, Gregory & Conrad (1938) removed the distichodontid genera *Xenocharax*, *Neolebias*, *Hemistichodus* and *Nannaethiops* to their subfamily Citharininae. More recently Poll (1973) carried this trend further by placing all distichodontids (*sensu* Greenwood *et al.*, 1966) into his family Citharinidae. Monod (1950), in turn, defined the suprageneric taxa among citharinids and distichodontids in such a manner as to exclude the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus* from all of his subfamilies. To the extent that these authors used their classifications as a mode of conveying concepts on the relationships between taxa, such differing classifications reflect the uncertainty that exists concerning the phylogenetic history of citharinids and distichodontids.

This uncertainty was a consequence of a series of factors, three of which appear to have been of paramount importance. Firstly, earlier classifications were based on a limited number of

Table 1 Previous classifications of the families Citharinidae and Distichodontidae with members of the suprageneric units listed where originally specified

Boulenger, 1909	Citharininae	*Citharinus*, *Citharidium*
	Distichodontinae	*Nannaethiops*, *Neolebias*, *Distichodus*, *Nannocharax*, *Xenocharax*
	Ichthyborinae	*Ichthyborus*, *Neoborus* (=*Phagoborus*), *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago*
Eigenmann, 1909	Citharininae	
	Neolebiinae	
	Distichodontinae	
	Phaginae	
	Ichthyborinae	
Regan, 1911	Citharininae	*Citharinus*, *Citharidium*
	Xenocharacinae	*Xenocharax*, *Nannaethiops*, *Neolebias*
	Distichodontinae	*Distichodus*, *Nannocharax*
	Hemistichodinae	*Hemistichodus*
	Ichthyborinae	*Ichthyborus*, *Neoborus* (=*Phagoborus*), *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago*
Gregory & Conrad, 1938	Citharininae	*Citharinus*, *Citharidium*, *Xenocharax*, *Nannaethiops*, *Neolebias*, *Hemistichodus*
	Distichodontinae	*Distichodus*, *Nannocharax*, *Ichthyborus*, *Mesoborus*, *Phagoborus*, *Eugnatichthys*, *Paraphago*, *Phago*
Greenwood *et al.*, 1966	Citharinidae	
	Distichodontidae	
	Ichthyboridae	
Poll, 1973	Citharinidae	*Citharinus*, *Citharidium*, *Xenocharax*, *Neolebias*, *Nannaethiops*, *Dundocharax*, *Congocharax* ?, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*
	Ichthyboridae	*Ichthyborus*, *Phagoborus*, *Gavialocharax*, *Hemistichodus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago*, *Belonophago*

primarily external characters. The utility of the limited information available from these systems was, however, reduced by several misinterpretations of characters and character states. Secondly, the small size of many distichodontid species resulted in a series of errors in character state determination. These errors were especially prevalent in the description of tooth form and distribution; characters which, nonetheless, were weighed heavily by many workers. Finally, and perhaps most importantly, generic and suprageneric taxa were defined on the basis of primitive or combinations of primitive and derived characters, a procedure which often failed to define monophyletic groups.

The present study attempts to determine the phylogenetic relationships, both at the generic and suprageneric levels, within the subunit of characoids formed by the families Citharinidae and Distichodontidae. The phylogenetic reconstruction is based primarily on osteological characters, although myological and other soft anatomical systems are also utilized. The three main objectives of this study are: (1) to test the hypothesis of the monophyletic nature of the unit formed by citharinids and distichodontids within characoids; (2) to determine the interrelationships of the genera within these families; and (3) to define the various generic and suprageneric taxa on the basis of shared derived characters.

Methods

Relationships between and within the families Citharinidae and Distichodontidae are evaluated using the methods of phylogenetic analysis first described in detail by Hennig (1966). These methods along with the two predominant alternative methodologies (numerical taxonomy and evolutionary biological classification) have been and continue to be a source of controversy with respect to their relative merits. However, the author feels that the Hennigian methodology best suits the aims of this study – the erection of an hypothesis of the evolutionary relationships of the groups in question.

In using the Hennigian or cladistic methodology, certain principles are followed: recognized taxa must be monophyletic in that they include all descendants of a hypothesized common ancestor (the concept of monophyly advanced by the evolutionary biological school, in contrast, does not require the inclusion in a taxon of all descendants of a common ancestor). Monophyletic groups are defined on the basis of shared derived (synapomorphic) characters which are considered to be the only type of characters valid for the erection of a hypothesis of common ancestry. In contrast, shared primitive (symplesiomorphic) characters and estimated degrees of similarity or difference are not utilized for the analysis of interrelationships. Species or species groups (two or more species forming a monophyletic unit) hypothesized to have had a common ancestor are termed sister species or sister groups. A derived (apomorphic) character used for the definition of a sister group relationship cannot serve for the definition of the contained taxa in either of the sister groups since it is primitive (plesiomorphic) at the level of the included subtaxa.

As discussed by Nelson (1973*a* & *b*), the apomorphic or plesiomorphic nature of characters can be evaluated by two methods. The first of these, outgroup comparisons, involves the examination of the state of the character in a variety of other groups in order to determine which of the relevant character states is probably primitive. For the purposes of this study, outgroup comparisons were carried out on representatives of other characoid families and selected non-characoid ostariophysans. The second method of character polarity determination involves information available from ontogenetic transitions. If in two sister groups X and Y, the species of group X undergo an ontogenetic transition in character A from state A to state A′, a transition that does not occur in the species of group Y, then two explanations exist for the distribution of the transition: (1) that the transition (state A to A′) was not present in the common ancestor of X and Y, but rather arose in lineage X; or (2) that the transition was present in the common ancestor of X and Y, but was secondarily lost in lineage Y. Comparing these hypotheses, we find that the first makes a single assumption; that of the acquisition of the transition in group X. The second in contrast, makes two assumptions, that of the presence of the transition in the common ancestor of groups X and Y, and a second assumption of its subsequent loss in lineage Y. If we accept a parsimony criterion for the evaluation of the preferability of alternative hypotheses, then the first, more parsimonious, hypothesis is preferable. Consequently, in this study, ontogenetic transitions (ontogenetic shifts from state A to state A′) are considered to indicate phylogenetic polarity (state A′ is considered apomorphic with respect to state A).

In the following discussion, osteological terminology follows Weitzman (1962) with several exceptions. As noted by Roberts (1969) vomer is substituted for prevomer and intercalar for opisthotic. Furthermore, I follow Patterson (1975) in using epioccipital rather than epiotic, and supraethmoid rather than ethmoid, and follow Nelson (1973*c*) in substituting angulo-articular for articular, and retroarticular for angular. Myological terminology is that of Winterbottom (1974).

All drawings were made using a Wild M5 drawing tube. Details were added freehand under higher magnification. Myological drawings are based on dissections of the right side of the specimen and are reversed into conventional orientation.

Materials

Osteological and soft anatomical systems were examined on alcohol preserved material, dry skeletons, and cleared, alizarin-stained specimens of representative species of the citharinid genera

Citharinus and *Citharidium* and the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Phago* and *Belonophago*. In the case of the monotypic distichodontid genus *Paraphago*, known only from the syntypic series, only osteological characters revealed by radiographs and external anatomy could be examined. Comparative studies were carried out on representatives of all other African and Neotropical characoid families and for certain characters on examples of the major non-characoid ostariophysan groups, both otophysan and anotophysan. A detailed listing of this extensive material would add little to the paper. Rather, a list of material examined, both skeletal and whole, quoting museum catalogue numbers, is deposited in the Fish Section and General Library of the British Museum (Natural History).

Abbreviations used in text figures

A_1	A_1 division of the *adductor mandibulae* muscle
A_{2-l}	lateral portion of the A_2 division of the *adductor mandibulae*
A_{2-m}	medial portion of the A_2 division of the *adductor mandibulae*
A_3	A_3 division of the *adductor mandibulae*
A_w	intramandibular (A_w) division of the *adductor mandibulae*
aa	angulo-articular
ac	anterior chamber of swimbladder
ant	antorbital
bo	basioccipital
cca	canal for coeliac artery
cl	cleithrum
cts	connective tissue sheath
den	dentary
DOP	*Dilatator operculi* muscle
dph	dorsal process of hyomandibula
ds	dermosphenotic
e	epibranchial
ep	epural
epi	epioccipital
ex	exoccipital
fr	frontal
h	hypural
hyf	hyomandibular fossa
hyo	hyomandibula
io	infraorbital
ico	independent coeliac ossification
ip	ischiac process
LAP	*levator arcus palatini* muscle
le	lateral ethmoid
les	lateral ethmoid strut
LP	*ligamentum primordiale*
max	maxilla
o	opercle
ops	opercular spine
orb	orbitosphenoid
os	os suspensorium
par	parietal
para	parasphenoid
pb	pharyngobranchial
pc	posterior chamber of swimbladder
pcl	postcleithrum
pdg	posterolateral dentary groove
pel	pelvic bone
ph	parhypural
plp	posterolateral preopercular process
pmp	posteromedial preopercular process
pmx	premaxilla
pop	preopercle
pro	prootic
psc	pterotic sensory canal
ptf	posttemporal fossa
pto	pterotic
pts	pterosphenoid
q	quadrate
ra	retroarticular
rt	replacement teeth
soc	supraoccipital
sor	supraorbital
sph	sphenotic
spo	suprapreopercle
T	tendon
ti	terminal section of intestine
up	upper pharyngeal tooth plate
ur	uroneural
vpv	ventral process of vertebra

Nomenclatural comments

The conclusions of this study necessitate several changes in the previous generic and suprageneric classifications within the family Distichodontidae. In so far as the modified terminology is used throughout the following discussion, these changes are briefly summarized at this point.

Within recent years, most workers have recognized two subfamilies (Distichodontinae and Ichthyborinae) or families (Distichodontidae and Ichthyboridae) for the unit termed the family

Distichodontidae in this work. However, the retention of both taxa as previously defined was found to be untenable under the taxonomic procedures adopted as a basis for this study. Rather only a single suprageneric taxon, the family Distichodontidae, is recognized to contain the species previously divided between the Distichodontidae and Ichthyboridae of Greenwood *et al.* (1966) and the subfamilies Distichodontinae and Ichthyborinae of many other recent workers. Similarly, the genera *Dundocharax* and *Congocharax* are placed as synonyms of *Neolebias*, with *Dundocharax bidentatus*, *Congocharax gossei*, *C. spilotaenia* and *C. olbrechtsi* hereafter termed *Neolebias bidentatus*, *N. gossei*, *N. spilotaenia* and *N. olbrechtsi* respectively. Finally, both *Gavialocharax* and *Phagoborus* are placed as synonyms of *Ichthyborus*, with *Gavialocharax monodi*, *Phagoborus ornatus* and *P. quadrilineatus* hereafter referred to as *Ichthyborus monodi*, *I. ornatus* and *I. quadrilineatus* respectively.

Phylogenetic analysis

The analysis of the phylogenetic relationships of the genera and suprageneric units within the complex formed by the families Citharinidae and Distichodontidae is divided into two sections. The first part of the analysis deals with the relevant characters in the various anatomical systems examined, along with a discussion of the basis for their hypothesized polarity within characoids. In the second portion of the analysis the evidence from these characters is incorporated into a reconstruction of the hypothesized most parsimonious phylogeny of the genera within these families. It should be emphasized that it is not the purpose of this study to provide detailed anatomical descriptions of the osteology and soft anatomy of all citharinid and distichodontid genera. Rather, only those characters used in the phylogenetic reconstruction are discussed.

Jaws

A series of modifications of the upper and lower jaws distinguish the unit formed by the Citharinidae and Distichodontidae within characoids and unite groups of varying levels of universality within this complex. The following discussion will deal firstly with the hypothesized derived characters common to the upper and lower jaws; secondly, with those limited to the lower jaw; and finally, with those of the upper jaw. Dental characters of phylogenetic interest are discussed separately in the following section.

Replacement tooth trenches

The form of the dentary and premaxillary replacement tooth trenches exhibits several character states among citharinids and distichodontids. In *Xenocharax* (Fig. 1a) the dentary and premaxilla are solid basally, with the replacement tooth trenches having the form of relatively shallow grooves, not or only slightly open to their partners across the symphyses. Such a trench form is close to the generalized and probably plesiomorphous characoid condition and is thus considered to represent the least derived state of this character within citharinids and distichodontids. Two major modifications of the *Xenocharax* form of replacement tooth trench occur in these families, one shared by most distichodontids and the other unique to citharinids.

The distichodontid genera *Nannaethiops* and *Neolebias* share with *Xenocharax* the plesiomorphous condition of shallow premaxillary and dentary replacement tooth trenches. In all other distichodontids, in contrast, the trenches are expanded, bulbous cavities, broadly open to their partners across the symphysis (Fig. 1b.) The expansion of the trenches into the primitively solid centres of the premaxilla and dentary both provides an increased surface for the attachment of the pleurodont dentition common to these genera, and space for their multiple rows of replacement teeth. Such a greatly expanded replacement tooth trench would appear to be unique to and apomorphous for these genera among characoids. In contrast, the greatly expanded trenches of the Neotropical characoid family Parodontidae differ from the above in being limited to the premaxilla, in not being open to each other across the symphyses, and in having the replacement tooth series separated by bony partitions. Similarly, the broad replacement tooth trenches of the Anostomidae fail to open to their partners symphyseally.

A second mode of expanded replacement tooth trench characterizes the family Citharinidae. In *Citharinus* and *Citharidium* the trenches are widened along the primitively horizontal plane of the dentaries and premaxillae to form broad shallow grooves. More significantly, the replacement tooth trenches of both jaws are rotated outwards relative to the *Xenocharax* condition. This reorientation is especially pronounced in the lower jaw where it has resulted in the shift of the primitively distal, anterior ridge of the trench to the outer surface of the dentary, and the formation of the distal edge of the lower jaw by the posterior ridge of the replacement tooth trench. Such a reorientation and broadening of the trenches appears to be unique to and autapomorphous for the Citharinidae among Characoids.

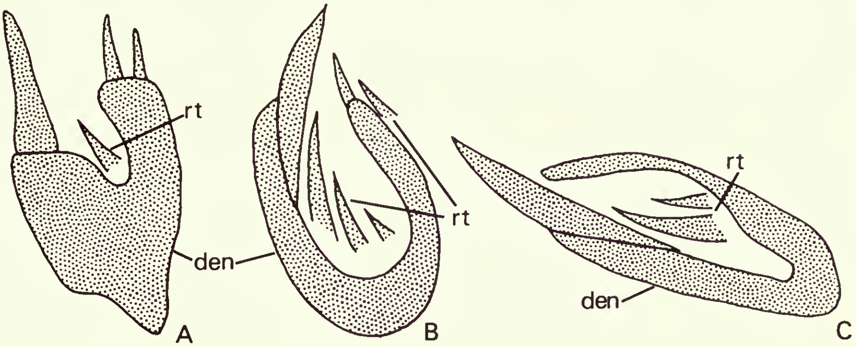

Fig. 1 Sagittal section through the dentary symphysis of A. *Xenocharax spilurus*, B. *Distichodus brevipinnis*, C. *Ichthyborus quadrilineatus*.

Lower jaw

A series of modifications of the dentary and of the articulation between the dentary and anguloarticular characterize various assemblages among citharinids and distichodontids. One of the distinctive characters in the lower jaws of these families is their common lack of the bony interdigitating symphyseal processes that interconnect the dentaries of most characoids. Such dentary interdigitations form a hinge permitting horizontal pivoting of the dentaries about the symphysis but reducing or eliminating twisting of the bones with respect to each other. This symphyseal dentary hinge ranges in complexity from the rather simple processes common to many tetragonopterines, to the massive interlocking systems in *Hydrocynus* (Gregory & Conrad, 1936) and the Cynodontini (Nelson, 1949). An interdigitating symphyseal dentary hinge is widespread among characoids and is found in the Hepsetidae, the family that has been considered to be the most 'primitive' living member of the Characoidea (Roberts, 1969, p. 442). If *Hepsetus* is indeed the sister group to other characoids, its possession of the dentary hinge along with the widespread distribution of this character within the Characoidea would indicate that an interdigitating symphyseal dentary hinge is plesiomorphous for characoids. The lack of such a joint would then be a apomorphous secondary loss. It should be emphasized, however, that the phylogenetic placement of hepsetids has not been satisfactorily resolved. Furthermore, an interdigitating dentary symphyseal joint is also lacking in the Neotropical characoid families Curimatidae, Hemiodontidae, Prochilodontidae, Anostomidae, Chilodontidae and Parodontidae. Be that as it may, at the least, the common lack of the interdigitating symphyseal dentary hinge in citharinids and distichodontids is consistent with the hypothesized monophyletic nature of the unit that they form within characoids.

Although the lack of an interdigitating dentary symphyseal hinge is common to all citharinids and distichodontids, the exact form of the interdentary articulation varies within these families. Citharinids and the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus* have a solely syndesmotic articulation between the dentaries. Within this assemblage, in *Citharinus*, *Citharidium*, *Xenocharax*, *Nannaethiops* and *Neolebias* the combination of the relatively limited contact of the dentaries across the symphysis and the syndesmotic joint permits a slight mobility of the dentaries relative to each other. In contrast, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus* have an immobile though syndesmotic interdentary joint as a consequence of their expanded replacement tooth trenches and the resultant greater cross-sectional contact across the symphysis. This union of the dentaries is further developed in some larger individuals of *Distichodus lussso* and *D. brevipinnis* which have irregular interdigitations between the dentaries (see Daget, 1959, Fig. 5).

The dentaries in the distichodontid genera *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* are synarthritically immovably interconnected in either of two ways. In *Ichthyborus* this union takes the form of a symphyseal fusion of the dentaries, an adaptation which provides a firm implantation for the enlarged median canine that characterizes this genus. *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Belonophago*, *Paraphago* and *Phago*, alternately, have a series of bony interdigitations uniting the dentaries. These interdigitations differ, however, from those forming the symphyseal dentary hinge of most characoids both in their location at the rear of the dentary symphysis and in rendering the dentaries totally immobile relative to each other. Both this synarthritic dentary articulation and the fused dentaries of *Ichthyborus* appear to be unique to their possessors among characoids and indicative of the monophyletic nature of each of these assemblages.

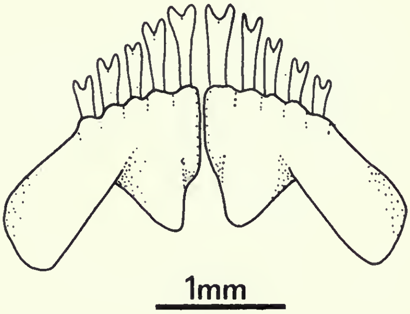

Fig. 2 *Nannocharax niloticus*, dentaries, ventral view.

Various modifications of the dentary serve to distinguish subunits within the family Distichodontidae. The genera *Hemigrammocharax* and *Nannocharax* are characterized by a pronounced posteriorly-directed process arising from the posteroventral edge of the dentary slightly lateral to the dentary symphysis (Fig. 2). This process, which serves as the point of attachment for the *protractor hyoidei* muscles, is unique to these genera among the characoids examined and is thus hypothesized to be apomorphous. *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in turn, have a prominent dorsally-directed posterodorsal dentary ramus that is laterally overlapped by, and tightly joined to, the closely connected maxilla and premaxilla common to these genera. Such a posterodorsal ramus of the dentary (Figs 3c & d) contrasts with the hypothesized plesiomorphous dorsally straight-edged process common to most characoids (Fig. 3a). Outgroup comparisons have failed to reveal any other charcoid group with such a pronounced development of this process. Thus the prominent posterodorsal ramus of the dentary common to these distichodontids is considered derived.

Further adaptations of this dentary ramus characterize less universal subunits of the Distichodontidae. In *Hemistichodus* this posterodorsal dentary ramus is autapomorphically further enlarged into an elongate, inwardly curved process passing medial to the premaxilla (see Daget, 1968, Fig. 2). *Eugnatichthys*, *Paraphago*, *Phago* (Fig. 3d) and *Belonophago*, in turn, have the lateral face of the ramus restructured to form a shallow groove articulating with the rounded posteroventral portion of the maxilla characteristic of these genera. This alteration of the dentary in conjunction with a series of modifications of the maxilla forms a sliding joint between the upper and lower jaws during jaw movements.

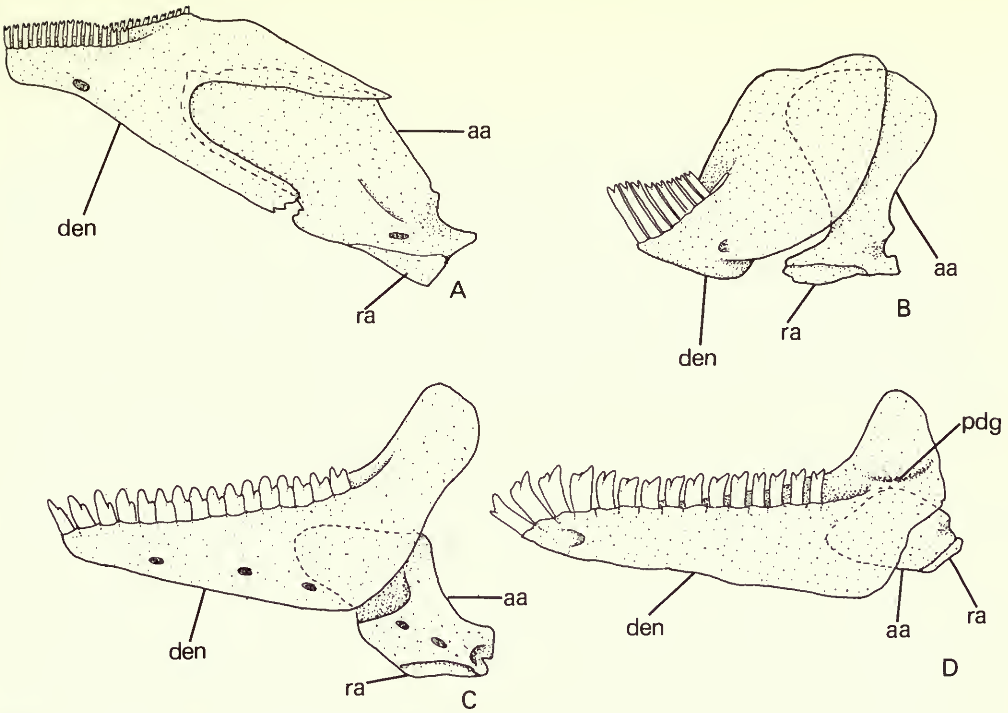

Fig. 3 Lower jaws of A. *Xenocharax spilurus*, B. *Distichodus notospilus*, C. *Ichthyborus quadrilineatus*, D. *Phago intermedius*, left lateral view.

The greatest morphological variation in the lower jaw of the families Citharinidae and Distichodontidae involves the form of the articulation of the dentary with the angulo-articular. In *Xenocharax* (Fig. 3a) the angulo-articular and dentary meet along an elongate triangular joint with the posteroventral process of the dentary bearing a lengthy mandibular sensory canal segment. The tight fit of this joint and the strong connective tissue bands across the articulation immovably join the dentary and angulo-articular into a single functional unit. Thus in *Xenocharax* all motion of the dentary relative to the suspensorium is a consequence of the mobility between the angulo-articular and quadrate. This form of articulation is generalized for characoids and most teleosts (see Nelson, 1973*c*), and undoubtedly represents the plesiomorphous condition for the Citharinidae and Distichodontidae. Such an immobile articulation is common to citharinids and the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus*. All other distichodontid genera, in contrast, have a mobile joint between the angulo-articular and dentary. The least restructured form of the articulation is found in *Hemistichodus* which retains the plesiomorphous insertion of the triangular anterior process of the angulo-articular into a notch formed by posterodorsal and posteroventral dentary processes. However, in contrast to the primitive condition, the dentary in *Hemistichodus* is not in tight contact with the anterior process of the angulo-articular and the connective tissue bands joining these bones are flexible. These modifications result in a limited mobility between the dentary and angulo-articular. Such motion approximates the hypothesized first stage in the phylogenetic development of the more mobile *Distichodus*, *Ichthyborus* and *Mesoborus* types of articulations between these bones.

The second form of mobile joint between the dentary and the angulo-articular, the *Distichodus* type (Fig. 3b) is synapomorphous for *Distichodus*, *Nannocharax* and *Hemigrammocharax* among characoids. In these genera the primitively elongate dentary is horizontally foreshortened and its posteroventral process greatly reduced. Furthermore, the axis of the body of the dentary is reorientated distinctly anteroventrally from the horizontal or anterodorsal orientation common to most characoids. This reorientation, which shifts the plesiomorphously anterior face of the dentary posteroventrally, is particularly pronounced in bottom-dwelling *Nannocharax* species which have a nearly vertical axis through the body of the dentary. An additional consequence of this dentary foreshortening and reorientation is the reduction of the dentary portion of the mandibular sensory canal in *Distichodus* and its loss in *Nannocharax* and *Hemigrammocharax*.

Congruent with these dentary alterations are a series of modifications of the angulo-articular and of its relationship to the dentary. In the *Distichodus* type lower jaw, the angulo-articular is expanded dorsally or anterodorsally into a large flat plate which lies along and is ligamentously movably attached to the medial face of the dentary. These alterations in angular-articular form and position together with the previously described dentary modifications result in a highly mobile joint between the dentary and angulo-articular, in addition to the usual mobility of the latter on the quadrate. This mode of articulation of these elements, the 'chevauchement lateral' of Monod (1950), along with the previously described reorientation of the dentary permits a marked degree of horizontal motion of the dentary.

The two final forms of mobile articulation between the dentary and angulo-articular, the *Ichthyborus* and *Mesoborus* types, share several derived characters. In both of these lower jaw forms the posteroventral ramus of the dentary is lacking as a distinct process contrary to its plesiomorphous elongate form. Congruent with this change in dentary structure is an anterior expansion of the angulo-articular and its shift onto the medial surface of the dentary. Such an expansion, which compensates for the loss of support primitively provided by the posteroventral dentary ramus, differs from that of the *Distichodus* type jaw in two ways. Firstly, the anterior process of the angulo-articular in the *Ichthyborus* and *Mesoborus* jaw forms is directed horizontally forward rather than having the dorsal or anterodorsal orientation that characterizes the *Distichodus* type jaw. Furthermore, rather than simply abutting the medial surface of the dentary the angulo-articular in these taxa inserts into a depression (*Ichthyborus*) or fossa (*Mesoborus* type) on the posteromedial surface of the dentary. These modifications and other adaptations permit an apomorphic greatly increased mobility between the dentary and angulo-articular.

The *Ichthyborus* type articulation (Fig. 3c) is specific to that genus and characterized by an elongate angulo-articular considerably thickened posterior to the rear margin of the dentary. This expanded posterior portion of the angulo-articular is undercut anteriorly to form a deep notch into which the posteroventral corner of the dentary fits. Both the thickening of the posterior portion of the angulo-articular and its relationship to the dentary are apomorphic characters seemingly unique to this genus among characoids. The *Mesoborus* form of articulation between the angulo-articular and dentary is common, with some variation, to *Mesoborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. In these genera the anterior portion of the angulo-articular inserts into a definite socket on the medial surface of the dentary. Along with the pronounced overlap of the dentary and angulo-articular, this adaptation shifts the pivot point of the dentary anteromedially. Within the assemblage characterized by the *Mesoborus* type articulation several subunits are distinguished by further modifications of the angulo-articular. In contrast to its plesiomorphously elongate state, the angulo-articular in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is a thickened element that is both shortened horizontally and shifted practically entirely onto the medial surface of the dentary (Fig. 3d). As a consequence the rear of the dentary extends nearly to the vertical through the joint of the angulo-articular with the quadrate. This apomorphic shortening of the angulo-articular is especially notable in *Eugnatichthys* in which the greatly thickened bone is barely visible laterally.

Keeping in mind the difficulties in determining the mode of action of a complex system on the basis of preserved material, it nonetheless appears that the two lower jaw pivot points (dentary-angulo-articular and angulo-articular-quadrate) in the *Ichthyborus* and *Mesoborus* jaw forms result in systems that are functionally unique among characoids. In *Ichthyborus* the ventral border of the dentary makes an oblique angle with that of the angulo-articular when the mouth is closed. As the mouth opens, the pivoting of the premaxilla on the supraethmoid causes the rear of the premaxilla to move ventrally. This motion is imparted *via* the reduced maxilla to the rear of the dentary. The entire lower jaw in turn shifts ventrally, with the dentary pivoting on the angulo-articular simultaneous with the pivoting of the entire dentary-angulo-articular complex on the quadrate. Both motions continue until the ventral borders of the angulo-articular and dentary achieve their plesiomorphous straight line orientation. During the second phase of jaw motion the mobility of the dentary relative to the angulo-articular ceases and these elements act as a rigid unit pivoting on the quadrate. Thus during the opening of the mouth, two functional phases are discernible; an apomorphic first phase characterized by mobility at both pivot points, and a second phase demonstrating only the plesiomorphous motion of the angulo-articular on the quadrate. Such a two-phase system is common to *Ichthyborus*, *Mesoborus* and *Microstomatichthyoborus*, and is the basis for the more derived jaw motion of *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* which have continual mobility between the angulo-articular and dentary throughout the entire cycle of jaw action. In these latter genera the ventral borders of the angulo-articular and dentary pass from the oblique concave angle of the closed jaw, to a straight-line orientation and then to a distinct convex relationship in the fully open mouth (see Gregory & Conrad, 1938, Fig. 35). This last apomorphic phase of the motion is, as far as can be determined, unique to these four genera among characoids.

Upper jaw

The plesiomorphous condition of the upper jaw in characoids appears to have the premaxilla immovably attached by tight syndesmotic articulations to the supraethmoid and lateral supraethmoid wings. Such attachment occurs either along the medial surface of the premaxilla (e.g. *Hepsetus*, *Acestrorhynchus*) or more usually to a posteriorly-directed ascending process of the premaxilla (e.g. *Brycon*, *Alestes*). Medially the premaxillae are completely or nearly completely separated symphyseally by an elongate supraethmoid spine. Plesiomorphously the maxilla is a moderately to markedly elongate element movably articulated with the posterodorsal edge of the premaxilla, and bearing anterodorsally a medially-directed process which attaches ligamentously to the palatine and *ligamentum primordiale*. Citharinids and distichodontids differ from this plesiomorphous upper jaw plan both in the relationships of the premaxilla with its partner and the supraethmoid, and in the form of the maxilla and its relationship to the premaxilla and dentary.

All citharinids and distichodontids lack the prominent premaxillary ascending process and tight connective tissue bands which plesiomorphously attach the premaxilla immovably to the supraethmoid. Instead a series of modifications of the premaxilla and supraethmoid result in a mobile articulation of the upper jaw with the supraethmoid. The various adaptations of the supraethmoid will be discussed in detail later in the paper. For the purposes of the discussion at this point, it suffices to note that among citharinids and distichodontids the plesiomorphous state of the forward edge of the supraethmoid is hypothesized to be an anteriorly trifurcate complex. In this condition a median plate extends anteriorly over the premaxillary symphysis, and ventrolateral articular processes insert into articular fossae on the rear of the premaxillae. In *Xenocharax* the articular fossa of the premaxilla has the form of a deep horizontal depression open to its partner across the symphysis and extending from the symphysis midway across the transverse width of the premaxilla. Such a horizontal fossa is hypothesized to be plesiomorphous for citharinids and distichodontids in so far as the corresponding horizontal supraethmoid process represents the least pronounced alteration of the primitively horizontal edge of the supraethmoid. Within citharinids and distichodontids, several derived modifications of this form of premaxillary fossa are found.

Among citharinids there occurs a progressive ontogenetic reduction of the roof of the basically *Xenocharax* form of articular fossa that characterizes juveniles of *Citharinus* and *Citharidium*. As a consequence in adult citharinids the fossa roof is reduced to a small shelf at the lateral margin of the depression. Thus the primitively ventral surface of the fossa is now exposed dorsally and is ligamentously attached to the median process of the supraethmoid. Such an attachment contrast with the latter's plesiomorphous attachment to the dorsal surface of the roof of the fossa.

Within the complex formed by *Distichodus*, *Hemigrammocharax* and *Nannocharax* there occurs a phylogenetic transition in the form, position and extent of development of the premaxillary fossa. *Distichodus notospilus* and *D. brevipinnis* have a basically *Xenocharax* form of wide horizontal fossa on the posterior surface of the premaxilla. In comparison in *Distichodus lusosso*, *D. niloticus* and *D. fasciolatus* the fossa is a conical pit located on the posterodorsal surface of the premaxilla. These adaptations are correlated with the posteroventral shift of the premaxillae in these species, a repositioning carried further in *Nannocharax* and *Hemigrammocharax*. In these latter genera the premaxillae are located distinctly ventral to the supraethmoid and the articular fossae are reduced either to small conical depressions on the dorsal surface of the premaxillae or are entirely lacking. An evidently independent shift of the fossa to the dorsal surface of the premaxilla occurs in *Hemistichodus* in which the articular fossa is a rounded groove on the posterodorsal surface of the premaxilla. Finally, in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* the articular fossa is a transversely directed pit on the medial surface of the longitudinally-oriented posterior portion of the premaxilla. This adaptation is especially pronounced in the last two genera.

The above modifications, those of the supraethmoid and a series of other alterations permit varying degrees of mobility of the premaxilla on the supraethmoid. Such motion is limited in citharinids but more pronounced in distichodontids, especially in *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. The upper jaw motion of these genera takes two forms. In *Distichodus*, *Nannocharax* and *Hemigrammocharax* the posteroventrally shifted premaxillae are notably mobile in the horizontal plane. In contrast, in the other distichodontids listed, the jaw modifications permit a pronounced pivoting of the premaxillae on the supraethmoid with a consequent increase in the vertical extent of the gape.

Among characoids other than citharinids and distichodontids, mobile premaxillary–supraethmoid articulations occur in the African characid genus *Hydrocynus*, and the Neotropical characoid families Anostomidae, Chilodontidae, Prochilodontidae, Parodontidae and Hemiodontidae (Roberts, 1974). *Argonectes* and *Bivibranchia*, in turn, have radically altered protrusible upper jaws in which the premaxilla separates from the supraethmoid during opening of the mouth. Comparison of the mobile upper jaw in *Hydrocynus* with that of citharinids and distichodontids reveals pronounced anatomical and functional differences between these systems. The consequent likelihood that these complexes represent independent acquisitions of upper jaw mobility is supported by the series of derived characters uniting *Hydrocynus* to African characids having immovable premaxillary–supraethmoid articulations (see Comments on the African Characidae). *Argonectes*, *Bivibranchia* and the family Hemiodontidae differ from citharinids and distichodontids both in their mode of premaxillary mobility and in their possession of a rhinosphenoid. The rhinosphenoid is a median orbital ossification unique to various South American characoid groups, most of which are characterized by a plesiomorphous immobile upper jaw. On the basis of the common possession of a rhinosphenoid and other characters, it is most parsimonious to assume that hemiodontids, *Bivibranchia* and *Argonectes* are closely related to Neotropical rhinosphenoid-bearing characoids with immovable upper jaws. In light of this, and the differences in the type of supraethmoid–premaxillary articulation, it appears that upper jaw mobility in these groups has been achieved independent of that in citharinids and distichodontids. Finally, prochilodontids, anostomids and the closely related chilodontids achieve upper jaw mobility by motion of the ascending arm (Anostomidae, Chilodontidae) or body (Prochilodontidae) of the premaxilla along the edge of the supraethmoid spine rather than *via* the citharinid and distichodontid type of hinging of the premaxilla on anterior processes of the supraethmoid. As such, the premaxillary mobility of these South American families appears to be non-homologous with that of citharinids and distichodontids. The closest approximation among charcoids to the citharinid and distichodontid type of premaxillary–supraethmoid articulation is found in the Neotropical family Parodontidae. The members of this family have a distinct dorsomedial premaxillary fossa articulating with anterolateral processes of the supraethmoid. However, as discussed in the Conclusions section, the parodontid fossa appears to be convergent with that of citharinids and distichodontids rather than an indicator of close relationship between the groups.

As was the case with the dentary symphysis, the interpremaxillary articulation among citharinids and distichodontids demonstrates several apomorphous modifications of varying levels of universality. Contrary to the plesiomorphous, limited syndesmotic contact of the premaxillae anterior to the supraethmoid spine citharinids and distichodontids have the medial surfaces of the premaxillae broadly in contact. Within these families, however, the exact form and extent of the contact varies significantly. In *Xenocharax*, *Nannaethiops* and *Neolebias* the combination of a syndesmotic joint and a somewhat narrow premaxillary symphysis permits a limited mobility between the premaxillae. Although retaining the plesiomorphous syndesmotic joint, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus* are immovably joined symphyseally. This immobility is a consequence of the expanded cross-sectional extent of the jaws around the widened replacement tooth trenches. Finally, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have a series of interdigitating convolutions at the rear of the premaxillary symphysis. This synarthritic joint eliminates all motion between the premaxillae, a trend that is carried further in *Ichthyborus monodi* in which the premaxillae are fused symphyseally. This fusion is, as far as can be determined, unique to this species among characoids and perhaps a function of its markedly elongate jaws.

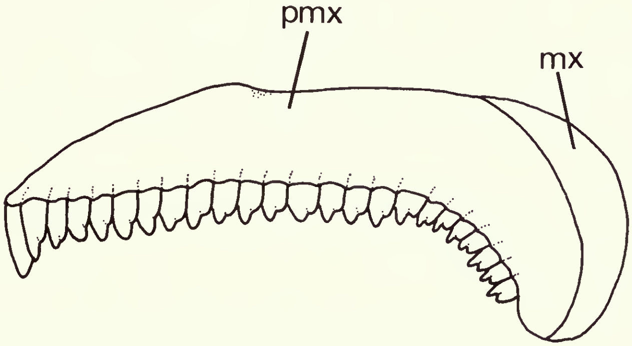

Fig. 4 *Ichthyborus quadrilineatus*, upper jaw, left lateral view.

A second form of synarthritic interpremaxillary joint characterizes the family Citharinidae. In *Citharinus* and *Citharidium* the longitudinal extent of the premaxillary symphysis is increased by the expansion of the median portions of the premaxillae posteriorly to form a prominent symphyseal bulge. This posterior expansion of the premaxillae along with a series of highly developed symphyseal interdigitations tightly join the premaxillae synarthrically. These premaxillary sutures differ, however, from those of some distichodontids both in the form and extent of the interdigitations, and in their association with the posteriorly expanded portion of the premaxilla. The consequent likelihood that the premaxillary sutures in the two groups are non-homologous is supported by the overall distribution of derived characters in these families.

Although the possession of interpremaxillary sutures is considered an apomorphous character on the basis of outgroup comparisons, such adaptations are not unique to citharinids and distichodontids within the Characoidea. Such sutures have been previously reported for the Neotropical genus *Brycon* (Weitzman, 1962) and the old world characid *Hydrocynus* (Eastman, 1917). Interpremaxillary sutures have also been found during this study in the South American characid genera *Triportheus* and *Serrasalmus*, and the African characids *Bryconaethiops* and *Alestes*. However, on the basis of a series of derived characters (the possession of a rhinosphenoid, tooth form and distribution, etc.) the South American genera appear to be most closely related to Neotropical characoids lacking interdigitating premaxillary sutures. Similarly, the old world groups form a monophyletic unit with African genera lacking the synarthritic joint (see p. 341). Consequently, the interpremaxillary suturing in these South American and African characoids appears to have been acquired independently of that in citharinids and distichodontids.

The final jaw character of interest is the form of the maxilla and its relationship to the premaxilla and dentary. The hypothetical plesiomorphous state of the maxilla among characoids is a relatively large, tooth-bearing element movably attached to the premaxilla, and with a dorsomedially directed process for the attachment of the palatine and *ligamentum primordiale*. In *Citharinus* and *Citharidium*, in contrast, the maxilla is relatively reduced but retains its mobility, flattened plate-like form and dorsomedially directed process. The maxilla in the distichodontid genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is also reduced. However, in these genera the relative reduction of the bone is much more pronounced than in citharinids. Furthermore, the maxilla in these genera is unique among characoids examined in its lack of a dorsomedial process and in being immovably joined, but not fused, to the rear of the enlarged premaxilla (Fig. 4). These maxillary alterations are most pronounced in *Hemistichodus* in which the bone is greatly reduced both relative to the generalized characoid condition and also with respect to that in the other genera listed. Furthermore, the maxilla in *Hemistichodus* is autapomorphically shifted onto the dorsal surface of the premaxilla (see Daget, 1968, Fig. 2) and is consequently totally removed from the ventral border of the upper jaw. Finally, the assemblage consisting of *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is characterized by a recontouring and expansion of the posteroventral portion of the reduced maxillary into a rounded somewhat bulbous process. During movements of the jaws this portion of the maxilla closely articulates with and slides along the previously described groove on the lateral surface of the posterodorsal dentary ramus.

In summary, the diverse apomorphic jaw modifications described above are:

1 the outward rotation of the replacement tooth trench in citharinids, and the great expansion of the trenches in distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.

2 the lack of an interdigitating symphyseal hinge joint in citharinids and distichodontids.

3 the fused dentaries of *Ichthyborus*.

4 the bony interdigitations along the posterior portion of the dentary symphysis in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

5 the posteriorly directed process lateral to the dentary symphysis in *Nannocharax* and *Hemigrammocharax*.

6 the pronounced posterodorsal dentary ramus in *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This process is laterally modified to form a groove articulating with the maxilla in the last four genera and is greatly developed autapomorphically in *Hemistichodus*.

7 the mobile joint between the dentary and angulo-articular in all distichodontids other than *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus*. The four forms of this mobile articulation are:

    (A) the *Hemistichodus* type limited to that genus and plesiomorphous with respect to the *Ichthyborus*, *Mesoborus* and *Distichodus* forms of the joint.

    (B) the *Distichodus* type occurring in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

    (C) the *Ichthyborus* type limited to that genus.

    (D) the *Mesoborus* type common to *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. The last four genera share an apomorphic further reduction of the horizontal extent of the angulo-articular.

8 the premaxillary articular fossa in citharinids and distichodontids.

9 the ontogenetic reduction of the premaxillary fossa roof in citharinids.

10 the reduction in the extent, and the shift of the articular fossa to the dorsal surface of the premaxilla in *Nannocharax*, *Hemigrammocharax* and some *Distichodus* species.

11 the rounded articular fossa on the dorsal surface of the premaxilla in *Hemistichodus*.

12 the laterally-directed articular fossa in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

13 the reduced maxilla of citharinids.

14 the greatly reduced, immobile maxilla in *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

15 the bulbous, posteroventrally expanded maxilla in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

16 the position of the maxilla on the dorsal surface of the premaxilla in *Hemistichodus*.
17 the interdigitating premaxillary symphyseal processes in citharinids and some distichodontids.

Dentition

Characoids are notable for, and largely classified on, the basis of their broad range in tooth form and arrangement. Such variation is evident in the morphology, distribution and mode of implantation of the dentition in the Citharinidae and Distichodontidae. Roberts (1967, p. 231) hypothesized that 'the most primitive dentition in characoids consists of conical teeth on the premaxillary, a single row of conical teeth extending beyond the gap of the maxillary, and two rows of conical teeth in the lower jaw separated by a shallow replacement trench'. Such a dental plan is consistent with our present knowledge of characoid ontogeny and phylogeny and would, with the exception of the tooth form, appear to have been the condition in the common ancestor of citharinids and distichodontids.

A bicuspidate equally-cusped tooth (Fig. 2) is common to all citharinids and distichodontids at some point in ontogeny. Multicuspidate dentition, either in the form of linearly arranged cusps (e.g. cheirodontines) or an arched cusp series along the edge of a wide tooth (e.g. *Brycon*, *Alestes*), is widespread among characoids. However, the bicuspidate tooth form of citharinids and distichodontids appears to be unique to, and apomorphic for, these families among characoids.

Within the Distichodontidae two assemblages have sequential ontogenetic replacement of the equally-cusped dentition by teeth demonstrating a relative enlargement of one cusp. In *Ichthyborus* this takes the form of a markedly developed anterior cusp, while *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have the posterior cusp enlarged. The shift from the equally-cusped tooth form, plesiomorphous for distichodontids, to the unequally-cusped condition can be followed ontogenetically in representative species demonstrating each form of enlarged cusp.

Among species with an enlarged anterior cusp, an ontogenetic series of *Ichthyborus besse* reveals a progressive shift to teeth with a relatively larger anterior cusp (Fig. 5a). In 30 mm SL specimens, the anterior cusp of the teeth at the front of each jaw is somewhat enlarged relative to the posterior cusp. This relative difference in cusp size decreases posteriorly so that the teeth at the rear of each jaw have equally-sized cusps. By 70 mm SL the anterior cusps of all teeth are larger than the posterior, with this difference again most pronounced anteriorly. Appreciably enlarged anterior cusps occur on all teeth in 100 mm SL specimens with the posterior cusp of the anterior teeth very small. *Ichthyborus besse* specimens of 150 mm SL have the posterior cusp on most teeth so reduced relative to the anterior cusp as to give the teeth a unicuspidate appearance. A similar, though not as pronounced, ontogenetic transition in tooth-cusp size occurs in *Ichthyborus ornatus* and *I. quadrilineatus* over the limited size range of specimens examined. It was not possible, however, to confirm the predicted ontogenetic transition in tooth form for *I. monodi* which is only known from adult specimens.

A size range of *Mesoborus crocodilus*, a species with an enlarged posterior tooth cusp, shows a progressive ontogenetic increase in the size of the posterior cusp (Fig. 5b). In 45 mm SL specimens the anterior teeth, particularly of the upper jaw, show a distinct enlargement of the posterior tooth cusp, with the remaining teeth retaining the plesiomorphous equally-cusped condition. By 55 mm SL nearly all the teeth in the upper jaw and those in the anterior half of the lower jaw exhibit an enlarged posterior cusp to varying degrees. At 70 mm SL the anterior cusp is totally lacking on the anterior teeth and greatly reduced on the remaining teeth of both jaws. The dentition of *Mesoborus* specimens of greater than 120 mm SL is nearly unicuspidate with a rudimentary anterior cusp remaining only on the posterior teeth of each jaw. It should be emphasized, however, that the relative difference in tooth cusp size found in *Mesoborus* is not universal among genera having an enlarged posterior tooth cusp. In *Microstomatichthyoborus* the posterior tooth cusp is only slightly enlarged. A slightly greater relative development of the cusp occurs in *Belonophago* (see Poll, 1957, Fig. 141), while *Eugnatichthys*, *Paraphago* and *Phago* show a marked enlargement of the posterior cusp, although the difference is not as appreciable as that of *Mesoborus*.

The mode of implantation of the outer tooth row also varies within the complex formed by citharinids and distichodontids. In all citharinids and the distichodontid genera *Xenocharax*, *Nannaethiops* and *Neolebias* the teeth attach by flattened or slightly oblique bases to a series of sockets along the distal edge of the replacement tooth trench ridges (Fig. 1a). Such an acrodont type of tooth attachment is generalized, though not universal, for characoids and tooth-bearing ostariophysans and is thus hypothesized to be plesiomorphous for citharinids and distichodontids.

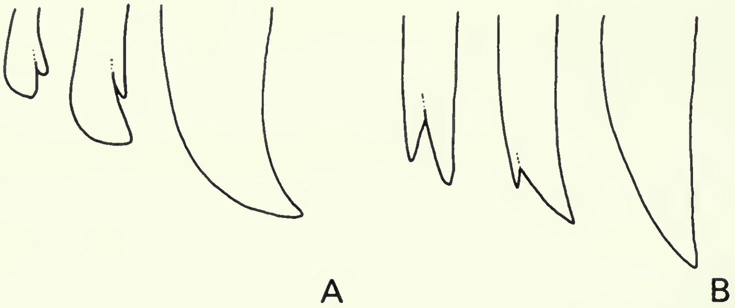

Fig. 5 Ontogenetic variation in dentition of A. *Ichthyborus besse* (fifth premaxillary tooth at 32, 50 and 115 mm SL), B. *Mesoborus crocodilus* (fourth premaxillary tooth at 55, 85 and 130 mm SL), left lateral view.

The outer row of dentition in all remaining distichodontid genera, in comparison, has the tooth form and mode of attachment illustrated in Figs 1b and c. In this condition, the teeth of the outer tooth row taper gradually to fit the anterior contours of the replacement tooth trench to which they have a ligamentous (pleurodont) attachment. As a consequence, the total relative length of the teeth is increased, with this elongation most pronounced in *Distichodus*, *Nannocharax* and *Hemigrammocharax*. The genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in turn, are characterized by relatively stronger teeth than those of citharinids and other distichodontids. Although the forward extension of the posterior wall of the replacement tooth trench results in what appear to be a series of interconnected sockets for the enlarged outer tooth row, in actuality these teeth retain their pleurodont attachment to the anterior wall of the trench (Fig. 1c).

The distribution pattern of the dentition within citharinids and distichodontids shows both reductions and increases relative to the previously described hypothetical plesiomorphous condition for characoids (see p. 275). The plesiomorphously present inner dentary tooth row is lacking in citharinids, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus* and all *Ichthyborus* species other than *I. besse*. On the basis of the hypothesized phylogeny (see p. 338) this absence of the inner row of dentary teeth appears, however, to have arisen *via* multiple independent losses. The opposite trend of an increase in the number of inner tooth rows on the dentary occurs in *Xenocharax* and some *Neolebias trilineatus* specimens (Daget, 1965, p. 7) which have two inner tooth rows, and in *Ichthyborus besse* where the inner row of dentary dentition is expanded into a broad band.

In the upper jaw, the dentition of both the premaxilla and maxilla varies within the assemblage formed by the Citharinidae and Distichodontidae. Contrary to the hypothesized plesiomorphous state of a tooth-bearing maxilla, citharinids and all distichodontids with the exception of *Xenocharax*, *Nannaethiops* and *Neolebias* have edentulous maxillae (the reported absence of maxillary teeth in some *Neolebias* species is erroneous, see p. 330). An inner premaxillary tooth row occurs in all distichodontids other than *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus ornatus* and *I. monodi*, all of which also lack the inner dentary tooth row. The lack of the inner row of premaxillary dentition in these taxa and in citharinids would appear to be apomorphous though considered to represent several independent losses on the basis of the hypothesized phylogeny. *Ichthyborus besse*, in contrast, has the inner row of premaxillary dentition expanded into a broad tooth patch. Finally, *Hemistichodus* is distinguished by the autapomorphous lack of the medial premaxillary teeth (see Poll, 1957, Fig. 134).

The final tooth character of phylogenetic interest among citharinids and distichodontids involves the canine dentition in *Ichthyborus* and *Mesoborus*. *Ichthyborus* has an enlarged unpaired tooth in the midline of the fused dentaries, an adaptation unique to this genus among characoids examined. The median dentary tooth and that flanking it on each side interdigitate with a pair of enlarged teeth at the anterior of the premaxillae (see Poll, 1957, Figs 132 & 136). In *Ichthyborus quadrilineatus* these dentary and premaxillary teeth are only slightly enlarged, with a limited overlap between the anterior teeth of the upper and lower jaws. However, in *I. ornatus*, *I. besse* and *I. monodi* these teeth are produced into prominent, significantly overlapping canines.

A different form of caniniform dentition characterizes *Mesoborus*. Although sharing with *Ichthyborus* an enlargement of the anterior premaxillary teeth, the dentary dentition in this genus is markedly different. *Mesoborus* lacks the unpaired median dentary tooth and the enlarged teeth flanking it that occur in *Ichthyborus*. Instead, the anteriormost dentary teeth of *Mesoborus* are quite small and the second to fourth teeth are strongly developed. These enlarged teeth arise from a distinct convex portion of the dorsal edge of the dentary and fit lateral to a series of relatively small teeth on a corresponding concave region of the premaxilla (see Gregory & Conrad, 1938, Fig. 34). Such a pattern of dentary and premaxillary dentition is not encountered elsewhere in the families under study, and is hypothesized to be derived relative to the graded dentition of most characoids.

In summary, the derived states of the dentition among citharinids and distichodontids are hypothesized to be:

1 the common possession in these families of a bicuspidate tooth. This tooth form is secondarily apomorphically modified by an enlargement of the anterior cusp in *Ichthyborus*, and of the posterior cusp in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

2 the pleurodont tooth attachment in all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.

3 the loss of maxillary teeth in citharinids and all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.

4 the loss of the inner dentary tooth row in *Nannocharax*, *Hemigrammocharax*, *Hemistichodus* and all *Ichthyborus* species other than *I. besse*.

5 the loss of the inner dentary tooth row in citharinids, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus ornatus* and *I. monodi*.

6 the lack of the medial premaxillary teeth in *Hemistichodus*.

7 the enlarged median dentary tooth of *Ichthyborus*.

8 the form of caniniform dentition in *Mesoborus*.

Supraethmoid

The supraethmoid form hypothesized plesiomorphous for characoids is an anteriorly triangular bone extending between, and completely or nearly completely separating, the premaxillae. The supraethmoid usually bears along its lateral margin a somewhat triangular process, the lateral supraethmoid wing, which is, however, lacking in many characoids with an elongate skull. As discussed previously, the supraethmoid of citharinids and distichodontids is greatly modified anteriorly as part of a system permitting upper jaw mobility. The least derived condition of the supraethmoid in these families occurs in *Xenocharax* in which the bone is relatively short longitudinally and lacks the plesiomorphously present lateral supraethmoid wings. More significant from a functional viewpoint are the marked modifications of its anterior edge. In contrast to the simple supraethmoid spine of the hypothesized plesiomorphous characoid state, in *Xenocharax* the supraethmoid is elaborated anteriorly into a wide trifurcate complex (Fig. 6a). Medially a short horizontal shelf extends forward from the anterodorsal edge of the supraethmoid to overlie and attach ligamentously to the dorsomedial portion of the premaxillae. On either side of, and slightly ventral to, this median process there is an anteriorly directed horizontal articular process which partially inserts into, and ligamentously attaches to, the previously described premaxillary fossa. As discussed earlier, the *Xenocharax* condition of a wide horizontal articular process is considered plesiomorphous for citharinids and distichodontids in that it represents the least derived modification of the primitively horizontal edge of the supraethmoid. Although the exact homology, if any, of the three supraethmoid processes with the primitively present supraethmoidal spine and lateral wings is unknown, these modifications of the anterior region of the supraethmoid appear to be apomorphous within characoids and as such are indicative of the monophyletic nature of the unit formed by the Citharinidae and Distichodontidae. The somewhat similar articular processes present in the South American characoid family Parodontidae differ in overall form and are considered to be independently acquired (see p. 340).

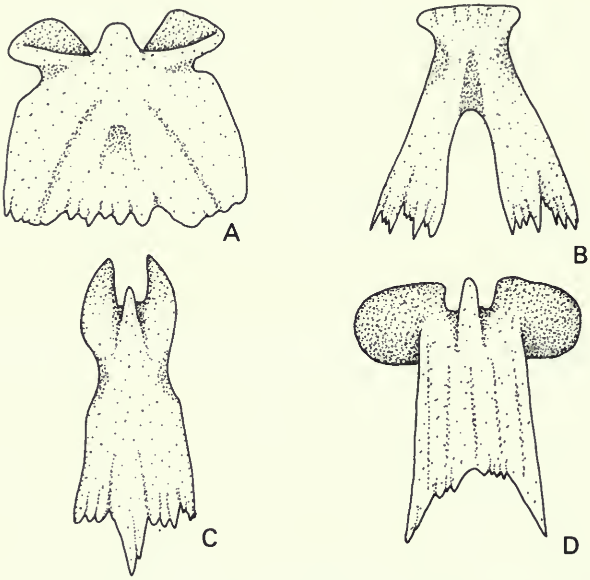

Fig. 6 Supraethmoid of A. *Xenocharax spilurus*, B. adult *Citharinus citharus*, C. *Distichodus niloticus*, D. *Phago loricatus*, dorsal view.

Various modifications of the *Xenocharax* form of supraethmoid distinguish the Citharinidae and subunits of the Distichodontidae. Juvenile citharinids have a basically *Xenocharax* type of supraethmoid with the anteromedial supraethmoid process overlying the premaxillae and prominent articular processes inserting into the premaxillary fossae. Congruent with the previously described ontogenetic alterations of the premaxillary fossae, citharinids demonstrate an ontogenetic increase in the extent of median supraethmoid process and a reduction of the lateral articular processes. The broad articular processes that are present in juvenile citharinids are progressively reduced along their lateral margins until the remaining medial portions coalesce with the enlarged median process. These alterations result in a single enlarged median supraethmoid process (Fig. 6b), in contradistinction to the juvenile anteriorly trifurcate supraethmoid. As a consequence of this restructuring of the supraethmoid and the correlated changes of the premaxillary articular fossa, in adult citharinids the enlarged median process of the supraethmoid overhangs and directly contacts the ventral surface of the articular fossa. Such an association contrasts with the plesiomorphous, and ontogenetically earlier, attachment of the median supraethmoid process to the dorsal surface of the fossa roof. In addition to the above adaptations of the anterior edge of the supraethmoid, *Citharinus* and *Citharidium* have the cranial fontanelle extending midway along the longitudinal extent of the bone. Such a forward extension of the fontanelle is lacking among distichodontids and rare among characoids in general. As such it is considered apomorphous for citharinids among characoids.

Several subunits of the Distichodontidae demonstrate distinctive modifications to the articular processes of the supraethmoid, and of overall supraethmoid form. In *Distichodus*, *Nannocharax* and *Hemigrammocharax* the median supraethmoid process is greatly reduced relative to the lateral articular processes. The latter, in turn, show a transition in form and orientation within these genera. The articular processes of *Distichodus notospilus* and *D. brevipinnis* retain the plesiomorphous flattened, horizontal form, although being somewhat more medially directed than in *Xenocharax*. The other *Distichodus* species examined, along with the genera *Hemigrammocharax* and *Nannocharax*, have the lateral articular processes modified into pointed, anteroventrally-directed prongs (Fig. 6c). In these taxa the articular processes either insert into a conical fossa on the posterodorsal face of the premaxilla (*Distichodus*) or attach ligamentously to the dorsal surface of that element (*Hemigrammocharax* and *Nannocharax*). Congruent with these alterations of the articular processes are changes in the overall form of the supraethmoid. Whereas the supraethmoid in *D. notospilus* and *D. brevipinnis* is relatively square, as it is in *Xenocharax*, those *Distichodus* species with prong-like articular processes have narrow elongate supraethmoids (Fig. 6c). This supraethmoid elongation and that of the articular processes appear to be correlated with the posteroventral shift of the premaxilla relative to the supraethmoid in these taxa. The distichodontid genus *Paradistichodus* also has a long, slender supraethmoid which in overall proportions resembles that of *Hemigrammocharax* and *Nannocharax*. However, contrary to the state of the supraethmoid in those genera. *Paradistichodus* retains the plesiomorphous condition of wide horizontal articular processes and a relatively large median process.

Two other supraethmoid modifications of note occur among distichodontids. In *Hemistichodus* the supraethmoid is greatly reduced to a small element totally lacking the median supraethmoid process, and with the articular processes rounded and laterally directed (see Daget, 1968, Fig. 3). Similarly, but evidently independently, the median supraethmoid process is reduced to approximately one-half of its plesiomorphous size in *Microstomatichthyoborus* and *Mesoborus*, and further diminished to a small pointed element in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Congruent with this reduction of the median supraethmoid process is an enlargement and reorientation of the articular processes in these genera. In *Microstomatichthyoborus* and *Mesoborus* these processes retain the plesiomorphous form of anteriorly-directed, horizontal plates. *Eugnatichthys* and *Paraphago*, in contrast, have less flattened articular processes that are both relatively larger and more distinctly orientated. Finally, in *Phago* and *Belonophago* the articular processes are markedly enlarged, bulbous, laterally-oriented structures (Fig. 6d).

The apomorphous modifications of the supraethmoid among citharinids and distichodontids are summarized as follows:

1 the anteriorly trifurcate form of the supraethmoid or a further derived state of the structure that is common to citharinids and distichodontids.

2 the reduction of the articular processes of the supraethmoid and their fusion with the enlarged median supraethmoid process in citharinids.

3 the reduction of the median supraethmoid process and restructuring of the lateral articular processes into pointed, anteroventrally-directed prongs in *Hemigrammocharax*, *Nannocharax* and some *Distichodus* species. Congruent with these changes, these taxa demonstrate a pronounced elongation of the supraethmoid.

4 the elongation of the supraethmoid in *Paradistichodus*.

5 the greatly reduced supraethmoid in *Hemistichodus*.

6 the progressive reduction of the median supraethmoid process, and the enlargement and lateral reorientation of the articular processes in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Anterior orbital region

The plesiomorphous condition of the anterior orbital region for characoids is hypothesized to have the orbitosphenoid separated from the lateral ethmoid. In this condition the olfactory nerve exits either from the anteromedian opening of the orbitosphenoid or through a foramen along its anterior face. The nerve then extends obliquely across the anteromedial region of the orbital cavity to the olfactory foramen of the lateral ethmoid. In contrast, citharinids and distichodontids, together with various South American and African characoid groups, have a direct contact of the lateral ethmoid and orbitosphenoid, with the olfactory bulb and tract covered laterally. In the following discussion the forms of this contact in the Citharinidae and Distichodontidae are first described and then contrasted to those in characoid outgroups.

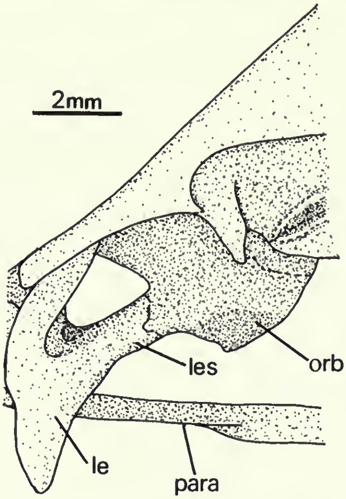

Fig. 7 *Xenocharax spilurus*, anterior orbital region, left lateral view.

Distichodontids other than *Nannaethiops* and *Neolebias* are characterized by the type of lateral ethmoid–orbitosphenoid contact illustrated in Fig. 7 or a further derived state of such an articulation. In the simplest condition, such as that of *Xenocharax*, the lateral ethmoid bears a prominent horizontal or posterodorsally sloping process which extends posteriorly from the postermedial portion of the lateral ethmoid to contact the anterolateral edge of the orbitosphenoid. This lateral ethmoid process forms a strut that laterally overlaps the olfactory bulb and tract and extends between the superior and inferior oblique muscles. As a consequence the entrance into the anterior myodome is horizontally divided posteriorly.

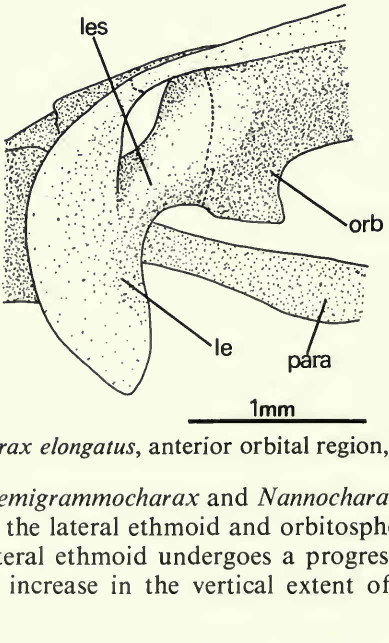

Fig. 8 *Nannocharax elongatus*, anterior orbital region, left lateral view.

The distichodontid genera *Hemigrammocharax* and *Nannocharax* share a further derived form of this type of contact between the lateral ethmoid and orbitosphenoid (Fig. 8). In these genera the posterior process of the lateral ethmoid undergoes a progressive vertical expansion phylogenetically, with a consequent increase in the vertical extent of the articulation between the lateral ethmoid and orbitosphenoid. Although the posterior process of the lateral ethmoid in *Hemigrammocharax monodi* and *Nannocharax multifasciatus* is vertically deeper than that occurring in *Xenocharax*, it is nonetheless distinctly separated dorsally from the ventral surface of the frontal. Thus these species retain a large opening dorsally for the passage of the superior oblique muscle into the anterior myodome. In *Nannocharax gobioides*, *N. fasciatus* and *N. intermedius*, however, the posterior process of the lateral ethmoid is greatly expanded vertically. This expansion both increases the vertical contact between the posterior process of the lateral ethmoid and the orbitosphenoid and further reduces the dorsal aperture into the anterior myodome.

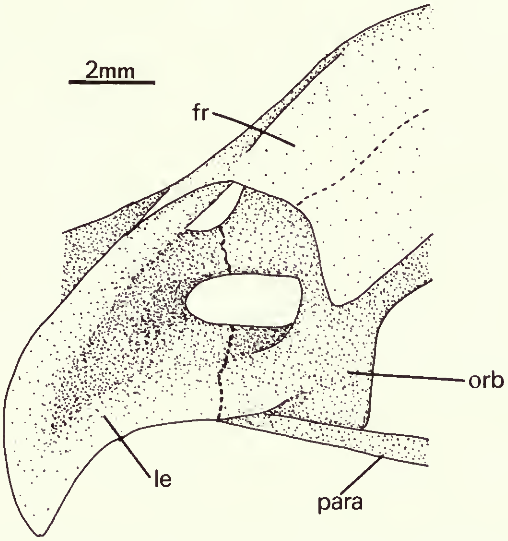

Fig. 9 *Citharinus citharus*, adult, anterior orbital region, left posterolateral view.

In contradistinction to the condition in all other distichodontids, the genera *Nannaethiops* and *Neolebias* lack any direct contact between the lateral ethmoid and orbitosphenoid. This absence of the lateral ethmoid strut is, however, hypothesized to be a secondary loss rather than a primary lack of such a structure. Such an hypothesis is congruent with the most parsimonious reconstruction of relationships among distichodontids, and with the myriad reductional trends demonstrated by the monophyletic unit formed by *Nannaethiops* and *Neolebias*. Furthermore, in *Nannaethiops unitaeniatus*, in which the reductional trends characteristic of these genera are least pronounced, there occurs a short posteriorly-directed lateral ethmoid process lateral to the olfactory foramen. This process may very well represent a reduced form of the *Xenocharax* strut.

The form of lateral ethmoid–orbitosphenoid contact common to all citharinids differs entirely from that in distichodontids. In *Citharinus* and *Citharidium* the orbitosphenoid is shifted to the anteroventral edge of the pterosphenoid as a consequence of the deep orbital lamella of the frontal characteristic of citharinids. The orbitosphenoid of citharinids extends ventrally, as a nearly vertical pillar, to contact the parasphenoid dorsally, and then continues forward as a large, anteriorly-directed, anterolaterally diverging process which articulates with a posterolateral process of the lateral ethmoid (Fig. 9). Juveniles of *Citharinus* and *Citharidium* possess solely this ventral bony contact of the lateral ethmoid and orbitosphenoid. In the anterodorsal region of the orbit, juvenile citharinids have a large cartilage block in the area between the anterior edge of the orbital lamella of the frontal and the posteromedial portion of the lateral ethmoid. This cartilage mass undergoes a progressive ontogenetic ossification from the anterodorsal portion of the orbitosphenoid. As a consequence in all larger citharinid specimens examined (*Citharinus latus*, *C. citharus*, *C. congicus*, *C. distichoides* and *C. gibbosus*) the area occupied earlier in ontogeny by the cartilagenous block is filled by a prominent process of the orbitosphenoid. This ossification extends anterior of the orbital lamella of the frontal along the ventral surface of that bone to either coalesce or synchondrally join with a smaller posterodorsal process of the lateral ethmoid. Although large specimens of all citharinid species were not available for examination, it appears that such an anterodorsal orbitosphenoid process probably occurs in the adults of *Citharidium* and other *Citharinus* species. These dorsal processes of the lateral ethmoid and orbitosphenoid, along with the aforementioned ventral articulation of these bones, restrict the entrance to the anterior myodome in citharinids to a single horizontally elongate fenestra.

Neither the dorsal nor the ventral articulation between the orbitosphenoid and lateral ethmoid among citharinids can be homologized with the bony lateral ethmoid strut joining these elements in most distichodontids. The distichodontid strut passes between the superior and inferior oblique muscles and arises directly lateral to the olfactory foramen through the lateral ethmoid. In citharinids, in contrast, the superior and inferior oblique muscles pass between the processes joining the orbitosphenoid and lateral ethmoid rather than around either or both of them. Furthermore, the lateral ethmoid olfactory foramen is located directly anterior to the central elongate fenestra between these processes, rather than medial to either of them. Consequently, other than by hypothesizing a highly complex series of alterations of the above bones, muscles and nerves, it is not possible to homologize either of the lateral ethmoid–orbitosphenoid contacts in citharinids with the bony lateral ethmoid strut of distichodontids. Thus it is most parsimonious to assume that the citharinid and distichodontid types of lateral ethmoid–orbitosphenoid articulation are distinct, independently acquired, apomorphous systems.

Outgroup comparisons have revealed various ostariophysan groups with articulations of the lateral ethmoid and orbitosphenoid somewhat similar to those of citharinids and distichodontids. Some of these in non-characoid ostariophysans (e.g. the bony tube between the orbitosphenoid and lateral ethmoid in the catfish *Diplomystes*) are undoubtedly convergent with those in the groups under discussion. Within characoids, however, a direct contact of the lateral ethmoid and orbitosphenoid occurs within African characids in *Hydrocynus*, *Bryconaethiops* and various *Alestes* species and in the Neotropical families Anostomidae, Curimatidae, Prochilodontidae, Paradontidae and Lebiasinidae. Consequently, the mere fact of a direct articulation between these bones is not a distinguishing character among characoids for either the citharinid or distichodontid type of contact. Nonetheless, in each case the particular form of lateral ethmoid–orbitosphenoid contact appears to be unique to citharinids and distichodontids among characoids.

The presence in distichodontids of a strut-like process between the orbitosphenoid and lateral ethmoid was noted by Starks (1926, p. 167) in *Distichodus fasciolatus*, *D. lusosso* and *Mesoborus crocodilus*. The same author also described a somewhat similar tubular process in the African characids *Alestes grandisquamis* and *A. liebrechstii*. This process of these characids was later noted for *Hydrocynus*, *Bryconaethiops*, *Alestes baremose*, *A. imberi* and *A. macrolepidotus* by Roberts (1969, p. 441), and has been found in *A. dentex* and *A. macrophthalmus* during these studies. Although the tubular process in African characids seems homologous with the distichodontid strut on a purely topographical basis, closer observation reveals several major differences between these structures. As previously noted, the distichodontid strut is formed primarily by the lateral ethmoid and covers only the lateral face of the olfactory bulb and tract. The process in the above characids, in contrast, is a bony tube formed primarily or entirely by the orbitosphenoid and completely surrounding the olfactory bulb and tract to varying degrees. Differences between these structures are also apparent in the phylogenetic and ontogenetic development of the orbitosphenoid tube of characids. Commencing in some *Alestes* species as a short anteriorly-directed lip around the orbitosphenoid olfactory foramen, the characid orbitosphenoid process becomes increasingly elongate anteriorly through the phylogenetic series until in *Hydrocynus* it is a thick tube extending to the rear of the lateral ethmoid. At no point during this phylogenetic sequence, or the similar ontogenetic transition of *Hydrocynus*, is there found a distichodontid type strut. Thus the characid tube and the distichodontid strut would appear to be analogous but non-homologous structures.

A closer approximation to distichodontid form of contact between the lateral ethmoid and orbitosphenoid occurs in the South American characoid family Parodontidae. Among parodontids, the genus *Saccodon* has a posterior lateral ethmoid process contacting the orbitosphenoid (see Roberts, 1974, Fig. 57). This lateral ethmoid process is rather similar to the *Xenocharax* strut between these elements. In *Parodon*, in contrast, the expanded contact between these bones is comparable to that of *Nannocharax*. These similarities are, however, considered to be convergent with those of distichodontids rather than an indicator of close relationship between the Parodontidae and Distichodontidae (see p. 340).

It is interesting to note that distichodontids and parodontids, together with the African characids having a bony tube between the orbitosphenoid and lateral ethmoid all have a forward shift of the olfactory bulb (see p. 341). It seems likely that the various adaptations of the anterior orbital region in these groups are correlated with this anterior position of the bulb and the consequent necessity to protect it from compression by the superior and inferior oblique muscles. Similarly, the dorsal and ventral articulations of the lateral ethmoid and orbitosphenoid in citharinids separate the olfactory bulb, nerve and tract from the orbital cavity and the inferior and superior oblique muscles. The only characoid found during this study to have a forward position of the bulb, but lacking some form of bony protection for it, was the Neotropical genus *Salminus*. However, in that genus the bulb is, nonetheless, surrounded laterally by a very heavy, inflexible connective tissue capsule.

An approximation to the citharinid form of contact between the orbitosphenoid and lateral ethmoid is found among the Neotropical families Anostomidae, Curimatidae, Prochilodontidae and Lebiasinidae. A variety of differences discriminate the form of contact in these families from that in citharinids. However, rather than dealing with these in detail, for the purposes of this study, it suffices to note that in none of them is the ventral articulation between the orbitosphenoid and lateral ethmoid as massive as in citharinids. Neither has there been found among these families any form of dorsal contact between the lateral ethmoid and orbitosphenoid comparable to that in citharinids.

Citharinids also demonstrate yet another modification of this region of the neurocranium. These genera have a prominent horizontal shelf extending along the rear portion of the orbitosphenoid and onto the anterior part of the pterosphenoid. The functional significance of this process, which is unique to *Citharinus* and *Citharidium* among the families under study, is presently unknown.

Derived states of the anterior orbital region among citharinids and distichodontids include:

1. the dorsal and ventral lateral ethmoid–orbitosphenoid contacts in citharinids.
2. the bony strut between the orbitosphenoid and lateral ethmoid in distichodontids. This strut is vertically expanded in *Nannocharax* and *Hemigrammocharax*, but is hypothesized to be secondarily reduced in *Nannaethiops* and *Neolebias*.
3. the shelf-like process on the lateral surface of the orbitosphenoid and pterosphenoid in citharinids.

Posterior orbital and anterior otic regions

Among citharinids and distichodontids the posterior orbital and anterior otic regions undergo a series of interrelated modifications and thus are most easily discussed as a unit. The plesiomorphous state of this portion of the neurocranium, within the complex formed by the Citharinidae and Distichodontidae, is hypothesized to be similar to that of *Xenocharax* (Fig. 10). This genus has the dorsal margin of the orbit formed by a distinct lateral process of the frontal. The posterodorsal wall of the orbital cavity is formed by the prominent sphenotic spine. This process extends distinctly lateral to the frontal and is orientated along the vertical through the trigemino-facialis foramen. Ventrolaterally the sphenotic bears a short vertical process which is continuous dorsally with the sphenotic spine, and ventrally with the prominent sharp-edged ridge of the lateral commissure of the prootic. This lateral commissural ridge, in turn, contacts the lateral flange present on the anterior edge of the ascending process of the parasphenoid. Together these lateral processes of the sphenotic, prootic and parasphenoid form a nearly continuous, laterally-directed flange at the rear of the orbital cavity. Along its ventral border the sphenotic forms the anterodorsal portion of the hyomandibular fossa which extends anteriorly to below the sphenotic spine and contacts the posterior edge of the orbital cavity. The prootic in *Xenocharax* is an angular element whose lateral surface nearly forms a right angle horizontally at the ridge of the lateral commissure. As a consequence the anterior portion of the prootic faces onto the orbital cavity while the posterior section contributes to the lateral surface of the neurocranium. In *Xenocharax* the prootic forms the dorsal and dorsolateral borders of the entrance into the posterior myodome, and the ventrolateral and ventral borders of the median opening into the braincase. Thus this bone broadly separates the posteroventral border of the pterosphenoid from the dorsal edge of the ascending process of the parasphenoid. Finally, the pterosphenoid and orbitosphenoid of *Xenocharax* are rather flat, square bones.

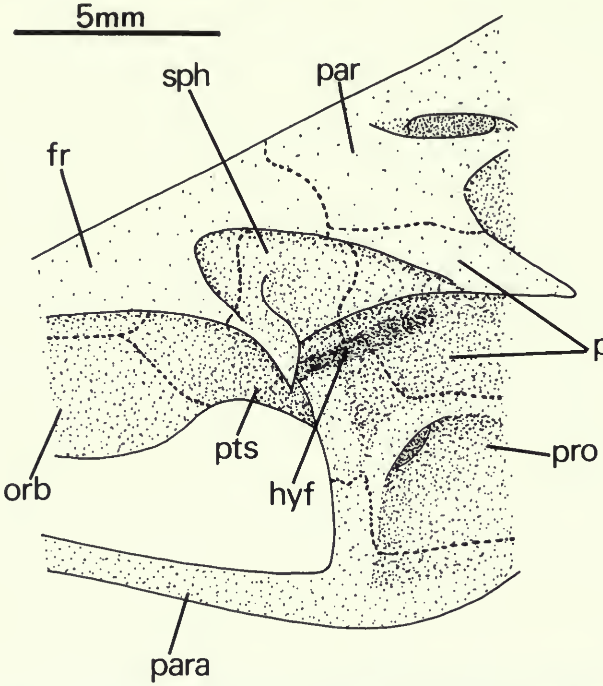

Fig. 10 *Xenocharax spilurus*, posterior orbital and anterior otic regions, left lateral view.

The *Xenocharax* plan of the posterior orbital and anterior otic regions agrees in general morphology, although not necessarily specific detail, with that in non-specialized members of most groups of characoids. Thus this plan is hypothesized to represent the plesiomorphous condition of this region for citharinids and distichodontids. Apart from a difference in the extent of the contribution of the supraorbital to the orbital rim (see p. 301), this arrangement of the posterior orbital and anterior otic regions is shared with minor variations by citharinids and the distichodontid genera *Xenocharax*, *Nannaethiops*, *Neolebias*, *Paradistichodus* and *Hemistichodus*. The remaining distichodontid genera can be divided into two assemblages on the basis of their distinct adaptations of this neurocranial region.

Within the subunit of distichodontids formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax* there occurs a progressive transition from the plesiomorphous ventrally sharp-edged sphenotic spine to a reduced, ventrally concave sphenotic process. *Distichodus* species such as *D. notospilus* retain the plesiomorphous condition of a large, nearly vertical sphenotic spine tapering ventrally to a thin edge. In *D. niloticus* and *D. fasciolatus* the central portion of the ventral edge of the spine is rotated slightly anteriorly, resulting in an oblique anteroventrally sloping central portion of the ventral margin of the spine. This alteration is further pronounced in species such as *D. lusosso* where this section of the sphenotic spine is expanded ventrally into a broad concave surface. Such a restructuring of the sphenotic spine is carried further in *Nannocharax* and *Hemigrammocharax* where the ventrally reduced spine has the form of a short, ventrally concave, posteroventrally sloping shelf.

The genera *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in turn, exhibit a different series of alterations and reductions of the bones of the posterior orbital and anterior otic regions (note: the osteology of *Paraphago*, known only from the type series of *P. rostratus*, was examined primarily by radiographs). Progressive modifications of several levels of universality characterize this region of the neurocranium among these distichodontids. In the following discussion these adaptations will be dealt with sequentially. First, those apomorphic alterations found in *Ichthyborus* and common to, or further modified in, the other genera listed above will be described. The further derived characters that characterize less universal groups within this unit will be discussed in light of the modifications in *Ichthyborus*.

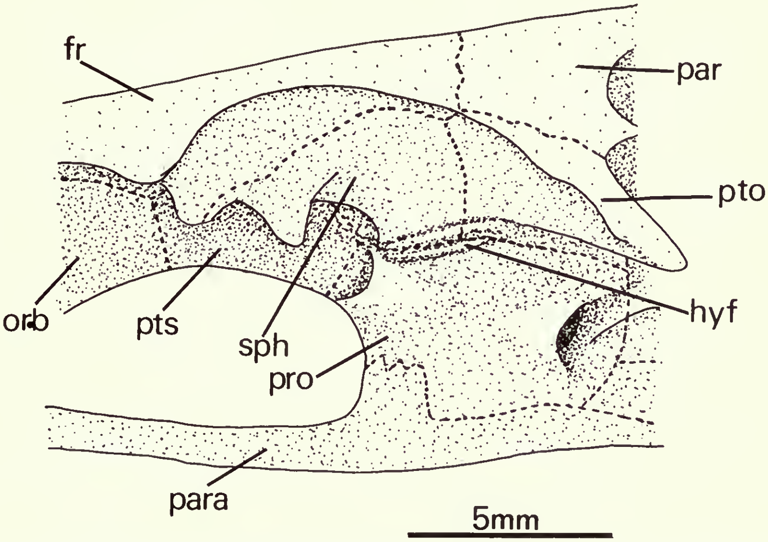

Fig. 11 *Ichthyborus besse*, posterior orbital and anterior otic regions, left lateral view.

The most pronounced alterations of this neurocranial region are those of the sphenotic, in particular the reduction and reorientation of the sphenotic spine. In *Ichthyborus* (Fig. 11), the entire sphenotic spine is rotated so that its primitively ventral edge is shifted posterodorsally. This reorientation results in the spine forming a posteroventrally sloping shelf in contrast to its plesiomorphous state of a nearly vertical wall. In addition, the lateral extent of the spine is reduced, resulting in a truncate process that barely extends beyond the lateral margin of the frontal. The overall form of the sphenotic in *Ichthyborus* is horizontally elongate relative to the hypothesized plesiomorphous state. Along with a posterior shift of the prootic, this elongation has resulted in a horizontal separation of the anterior margin of the hyomandibular fossa from the posterior edge of the sphenotic spine and the vertical through the trigemino-facialis foramen. Such a separation is considered derived relative to the close approximation of these structures in the plesiomorphous condition. The prootic of *Ichthyborus* is also markedly restructured from the plesiomorphous condition in which the lateral commissure bears a sharp-edged lateral ridge. In this genus the prootic is a gently curved, flattened element unelaborated laterally apart from the slightly raised lips around the facialis and trigemino-facialis foramina. The prootic of *Ichthyborus* is also shifted posteriorly, resulting both in the aforementioned repositioning of the hyomandibular fossa and in the reduction of the contribution of the prootic to the edge of the opening into the posterior myodome. As a consequence of the latter change, there is a significant reduction in the plesiomorphously wide separation between the posterior border of the pterosphenoid and the ascending arm of the parasphenoid.

The final noteworthy adaptation of this neurocranial region in *Ichthyborus* involves the ventral surface of the orbital process of the frontal. In citharinids and most distichodontids that portion of the frontal forming the roof of the orbital cavity is a ventrally smooth, slightly concave surface; a condition probably plesiomorphous for characoids. The ventral surface of the frontal in *Ichthyborus*, in contrast, bears a strong transverse ridge capped laterally by an anterodorsal extension of the sphenotic spine. This ridge is continuous with the orbital lamella of the frontal and extends transversely along the ventral surface of the bone just anterior to the suture of the frontal with the anterodorsal edge of the sphenotic spine.

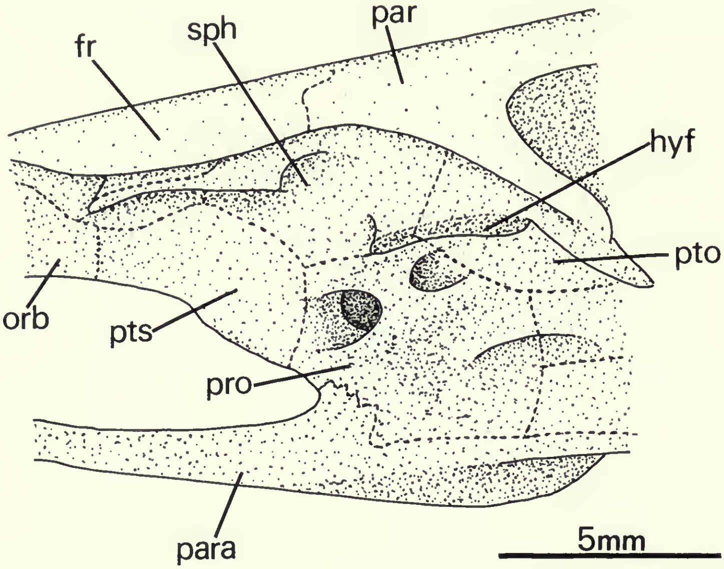

Fig. 12 *Mesoborus crocodilus*, posterior orbital and anterior otic regions, left lateral view.

These apomorphous modifications of the posterior orbital and anterior otic regions are common to *Ichthyborus* and *Microstomatichthyoborus*, and are the basis for a series of further derived adaptations in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Congruent with the overall elongation of the neurocranium, the orbitosphenoid and pterosphenoid of these latter genera are notably elongate both relative to the *Ichthyborus* condition, and more notably with respect to the hypothesized plesiomorphous characoid state. These taxa also have in common a further restructuring of the sphenotic spine. The primitively ventral edge of the sphenotic has rotated posterodorsally nearly to the level of the horizontal through the anterodorsal margin of the spine. Thus in these genera the spine has the form of a nearly horizontal shelf (Figs 12, 13, 14) rather than the near vertical wall at the rear of the orbital cavity of *Xenocharax*, or the posteroventrally slanting process of *Ichthyborus*. As described earlier, the plesiomorphous sphenotic spine extends distinctly lateral to the edge of the frontal, with *Ichthyborus* having the lateral extent of the spine significantly reduced. *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* show a further reduction of the *Ichthyborus* form of the sphenotic. In *Mesoborus* the sphenotic spine barely extends lateral of the edge of the frontal, and it falls distinctly short of the margin in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Within the latter assemblage, the anterior sphenotic process which caps the transverse ridge of the frontal is significantly reduced in *Eugnatichthys* and completely lost in *Phago* and *Belonophago* (the condition of the process is unknown in *Paraphago*). In addition, *Belonophago* lacks, evidently secondarily, the transverse strut along the ventral edge of the frontal that characterizes other members of its monophyletic unit.

Phago and *Belonophago* can be further distinguished within distichodontids by the broad contact between the posteroventral portion of the pterosphenoid and the dorsal margin of the ascending arm of the parasphenoid (Fig. 14). The extensive articulation between these bones totally separates the prootic from its plesiomorphous location along the anterior margin of the entrance into the posterior myodome. Furthermore, radiographs of *Paraphago rostratus* reveal what appears to be a less extensive suture between these bones. Therefore *Phago*, *Belonophago* and perhaps *Paraphago* share a synapomorphous contact of the pterosphenoid and parasphenoid.

Belonophago is a highly specialized genus characterized by long jaws and an extreme elongation of the skull, particularly in the posterior orbital region (Fig. 14). In this genus the pterosphenoid is expanded posteriorly and ventrally to form the entire anterior surface of the braincase. As a consequence of this elongation, the lateral commissure and hyomandibular fossa are markedly shifted posteriorly and are removed from the rear of the orbit by a distance equal to the orbital diameter. Such an extensive separation is derived relative to the *Ichthyborus* condition of a slight distance between these structures, and is a pronounced apomorphous change relative to the plesiomorphous close proximity of the anterior portions of the lateral commissure and hyomandibular fossa to the rear of the orbital cavity. As noted previously, the pterosphenoid in *Belonophago* is broadly in contact posteroventrally with the ascending process of the parasphenoid. In addition, *Belonophago* has a median articulation between these elements. Arising from the anterior face of the pterosphenoid is a ventrally-directed medial process which contacts a corresponding dorsally-orientated medial parasphenoid strut. Together these processes form a pedicle between the pterosphenoid and the parasphenoid (Fig. 14), an adaptation that is evidently unique to this genus among characoids.

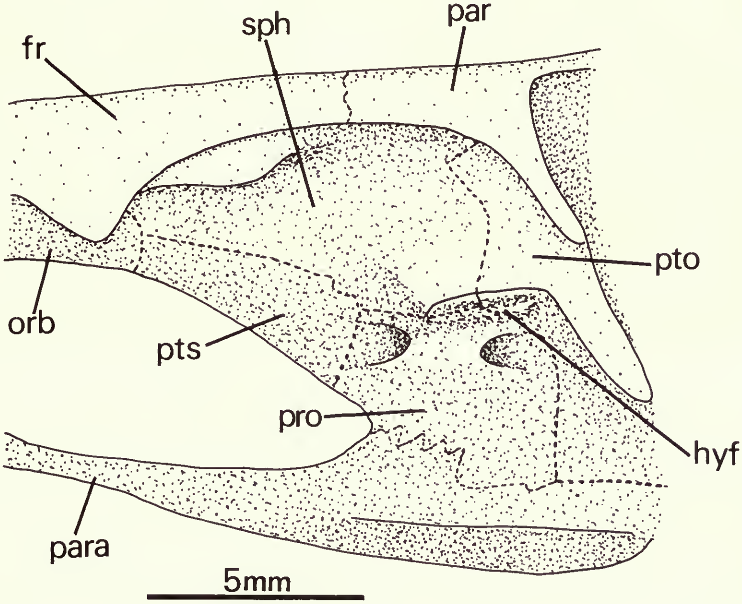

Fig. 13 *Eugnatichthys eetveldii*, posterior orbital and anterior otic regions, left lateral view.

A series of autapomorphous adaptations of the posterior orbital and anterior otic regions distinguish *Eugnatichthys* among distichodontids. The pterosphenoid in this genus is shifted posteroventrally by the ventral expansion of the orbital lamella of the frontal. This shift, along with the horizontal elongation of the sphenotic, results in a marked separation, both vertically and horizontally, between the rear of the sphenotic spine and anterior margin of the hyomandibular fossa. Together with a horizontal expansion of the pterosphenoid, this sphenotic elongation has shifted the prootic and associated lateral commissure posteriorly relative to the *Ichthyborus* condition. Although *Eugnatichthys* and *Belonophago* both possess a pronounced posterior shift of the hyomandibular fossa and lateral commissure, the method by which this realignment is achieved differs greatly in the two genera. In *Eugnatichthys* this restructuring is primarily a consequence of the elongation of the sphenotic and the ventral expansion of the orbital lamella of the frontal. In *Belonophago*, in contrast, the realignment is largely the result of the horizontal extension of the pterosphenoid.

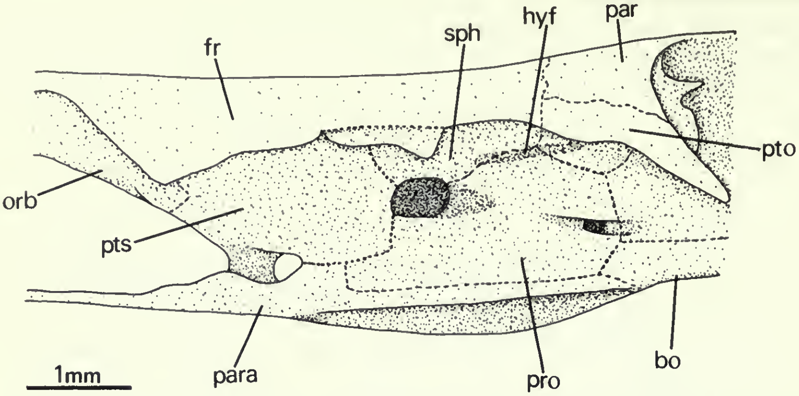

Fig. 14 *Belonophago tinanti*, posterior orbital and anterior otic regions, left lateral view.

Several modifications of the parasphenoid are of interest for an understanding of relationships within the Citharinidae and Distichodontidae. The plesiomorphous characoid parasphenoid form appears to be a flat, straight or ventrally convex element, extending posteriorly to below the basioccipital. In *Citharinus* and *Citharidium*, in contrast, the parasphenoid is markedly flexed ventral to its ascending processes and ontogenetically develops a bulbous process ventral to this point of flexure. This process serves as the area of attachment for the anteriorly shifted suspensory pharyngeals characteristic of this family. Posteriorly the citharinid parasphenoid has two slightly divergent lateral wings separated by a deep groove. Although such a condition occurs in many characoids in which the posterior myodome is posteroventrally open, in citharinids the myodome is closed at the rear, and the posterolateral wings of the parasphenoid surround the anterior portion of the dorsal aorta. In juveniles of *Citharinus* and *Citharidium* these parasphenoid processes are separate both from the basioccipital and the highly modified pars sustentaculum of the Weberian apparatus. In adults, however, the posterior parasphenoid processes fuse dorsally with the basioccipital and posteriorly with the ventral projections of the pars sustentaculum (see discussion on the Weberian apparatus). The overall modifications in pharasphenoid form, and the changes in its relationships to the basioccipital and pars sustentaculum are hypothesized to be apomorphous.

The distichodontid genera *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have the parasphenoid expanded ventrally into a flattened median ridge. This process serves as a point of attachment for the posteroventrally shifted suspensory pharyngeals occurring in these genera and is most developed in *Eugnatichthys* in which the shift is most pronounced (Fig. 13).

In summary, the hypothesized apomorphous states of the posterior orbital and anterior otic regions in citharinids and distichodontids include:

1 the vertical reduction and horizontal expansion of the sphenotic spine in *Hemigrammocharax*, *Nannocharax* and some *Distichodus* species. The restructuring of the spine is particularly pronounced in the first two genera.

2 the lack of lateral flanges on the prootic and ascending arm of the parasphenoid in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera also share a laterally reduced sphenotic spine whose plesiomorphously ventral edge is shifted posterodorsally; the development of a transverse process on the ventral surface of the frontal; a posterior shift of the hyomandibular fossa; and a reduction in the gap between the parasphenoid and pterosphenoid.

3 the restructuring of the sphenotic spine to form a horizontal shelf in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. The lateral extent of the spine is slightly further reduced relative to the *Ichthyborus* condition in *Mesoborus*, and greatly so in the other genera listed.

4 the reduction of the sphenotic process capping the transverse process of the frontal in *Eugnatichthys*, and its loss in *Phago*, *Belonophago* and perhaps *Paraphago*.

5 the broad articulation between the pterosphenoid and parasphenoid in *Phago*, *Belonophago* and perhaps *Paraphago*, with *Belonophago* having an autapomorphous median contact between these elements.

6 the pronounced posterior expansion of the pterosphenoid in *Belonophago*.

7 the ventral expansion of the orbital lamella of the frontal and a horizontal lengthening of the sphenotic in *Eugnatichthys*.

8 the distinctive flexure in the parasphenoid and the development of a ventral bulbous parasphenoid process in citharinids. In these genera the posterior processes of the parasphenoid straddle the dorsal aorta and fuse with the pars sustentaculum and basioccipital.

9 the median ventral parasphenoid ridge in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Occipital region

The character of phylogenetic interest in the occipital region of citharinids and distichodontids is the number, form and extent of development of the posttemporal fossae. The most widespread, and the hypothesized plesiomorphous, state of these openings among characoids consists of a dorsal and posterolateral pair of fossae on either side of the neurocranium. The horizontal or slightly oblique dorsal fossa is bordered by the supraoccipital medially, the parietal anteriorly and the epioccipital posteriorly. The remaining fossa is located at the posterolateral corner of the neurocranium and is bordered anteriorly and ventrally by the pterotic, and posteriorly and dorsally by the epioccipital.

Citharinids and distichodontids, in contrast, also possess an additional vertically ovate fossa bordered by the epioccipital and exoccipital (Fig. 15) (citharinids although possessing this 'third' fossa have, however, lost the dorsal fossa and thus retain only two sets of openings, see below). On the basis of outgroup comparisons the possession of a third fossa appears to be derived among ostariophysans in general and characoids in particular. However, although not widespread, a third posttemporal fossa *per se* is not unique to citharinids and distichodontids among charcoids. Such a feature has been found in most African characids and among South American characoids in the families Curimatidae, Hemiodontidae (Roberts, 1974), Parodontidae (Roberts, 1974) and the characid tribe Cynodontini (*sensu* Howes, 1976). However, the third posttemporal fossa in these taxa, with the exception of the Cynodontini, is a small round opening entirely within the epioccipital. This condition contrasts with the large ovoid fossa bordered by the deeply incut exoccipital and epioccipital in citharinids, distichodontids and cynodontines.

Although the Cynodontini possess a form of third posttemporal fossa very similar to that of citharinids and distichodontids, they do not, however, appear to be the sister group to the latter families. As discussed by Howes (1976), cynodontines possess a series of derived characters uniting them to the neotropical characid tribe Characini which lacks a third posttemporal fossa. Furthermore, the members of both the Cynodontini and Characini have a rhinosphenoid, an element unique to various South American characoids, most of which lack any form of third posttemporal fossa. In light of the lack of the third fossa both in the sister group to cynodontines and in the more inclusive unit of Neotropical characoids defined by the presence of a rhinosphenoid, it is most parsimonious to assume that the cynodontines arose from an ancestor possessing a rhinosphenoid but lacking a third posttemporal fossa. It thus appears that although convergently derived in cynodontines, the possession of a vertically ovate third posttemporal fossa bordered by the epioccipital and exoccipital is apomorphous for, and indicative of the monophyly of the unit formed by citharinids and distichodontids within characoids.

The genera *Citharinus* and *Citharidium* lack the plesiomorphously present posttemporal fossa on the posterodorsal surface of the neurocranium. In *Eugnatichthys*, in turn, there occurs a greatly reduced fossa in the same area. Both the reduction of the fossa in *Eugnatichthys* and its loss in citharinids are considered derived in so far as the possession of a large dorsal posttemporal fossa is generalized among characoids.

Cranial fontanelle

The extent of the dorsomedian fontanelle varies considerably within the unit formed by citharinids and distichodontids. Although the plesiomorphous condition of the fontanelle for these families or indeed any otophysans is difficult to ascertain, this variation does permit certain assumptions to be made. Of particular note is the extension of the fontanelle into the posterior half of the supraethmoid in *Citharinus* and *Citharidium* (Fig. 6c). Such an elongate fontanelle is rarely encountered among characoids and appears apomorphous for the superfamily. Among distichodontids, *Xenocharax* possesses an elongate fontanelle that separates the frontals, which are only in contact at the epiphyseal bar, and the parietals. The remaining distichodontids demonstrate a progressive phylogenetic reduction of this extensive fontanelle. All distichodontids apart from *Xenocharax* have a shorter opening which at the maximum extends slightly anterior to the epiphyseal bar. *Ichthyborus*, *Microstomatichthyoborus*, *Belonophago*, *Mesoborus*, *Eugnatichthys*, *Paraphago* and *Phago* have a further reduced fontanelle limited to the interparietal region, with this reduction particularly pronounced in the last four genera. The hypothesis that a progressive reduction of the fontanelle is apomorphic among distichodontids is congruent with the large fontanelle that characterizes the Citharinidae, the family which is hypothesized as the sister group to distichodontids. Such a hypothesis also agrees with the distribution of a large suite of derived characters within distichodontids. This reductional trend appears, however, to have been slightly reversed in *Belonophago* where the fontanelle is enlarged relative to the condition in other members of its monophyletic group.

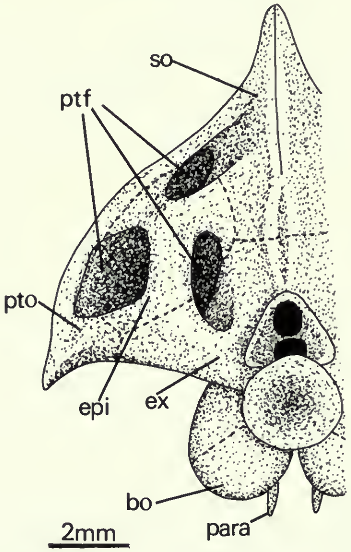

Fig. 15 *Xenocharax spilurus*, neurocranium, posterior view.

Suspensorium

The diverse modifications of the dentition, jaws and neurocranium that characterize the Citharinidae and subunits of the Distichodontidae are reflected in a series of alterations to the suspensorium. Two different types of suspensorium can be discriminated among citharinids and distichodontids on the basis of the relative position of the articulation of the angulo-articular with the quadrate. In *Citharinus*, *Citharidium*, *Xenocharax*, *Neolebias* and *Nannaethiops* the horizontal distance between the ventral portion of the hyomandibula and the articular condyle of the quadrate is relatively short. As a consequence, the articulation of the angulo-articular with the quadrate occurs below the centre of the orbit and distinctly posterior to the vertical through the body of the lateral ethmoid. In the remaining distichodontid genera, in contrast, the symplectic, metapterygoid and quadrate are relatively elongate resulting in a forward shift of the articular condyle of the quadrate to below or anterior to the vertical through the lateral ethmoid.

The polarity of such changes in the position of the articulation of the angulo-articular with the quadrate is somewhat problematical in that both anterior and posterior positions of this joint occur within a variety of seemingly monophyletic characoid groups. Consequently, a shift in the position of the articulation has evidently occurred independently within the Characoidea on several occasions. It is nonetheless interesting to note that those characoid groups which have been considered to be 'primitive' (Hepsetidae and Erythrinidae) have the posterior position of this joint; a location also common to generalized members of most characoid groups. If these families do indeed possess the plesiomorphous jaw form, then the primitive joint position and type of suspensorium among citharinids and distichodontids would be the posterior articulation common to *Citharinus*, *Citharidium*, *Xenocharax*, *Neolebias* and *Nannaethiops*. It is furthermore noteworthy that distichodontids with an anterior articulation of the quadrate and angulo-articular have derived forms of jaws and dentition. This congruence of the forward position of the angulo-articular-quadrate joint with a series of apomorphous jaw characters, contrasted with the posterior articulation among 'primitive' and generalized characoids, supports the hypothesis that an anterior articulation of these elements is the derived condition.

These adaptations in the suspensorium are reflective of the relative mouth sizes of the two groups of genera. In characoids with a non-protrusible mouth, the length of the jaws and consequently the extent of the gape is primarily a function of the position of the articulation of the quadrate with the angulo-articular. Thus in small-mouthed characoids the joint occurs under or forward of the ventral process of the lateral ethmoid. In large-mouthed, often predacious forms, in contrast, the articulation is distinctly posterior to the lateral ethmoid, and is sometimes also shifted ventrally. The distichodontid genera *Hemistichodus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Ichthyborus*, *Paraphago*, *Phago* and *Belonophago*, particularly the latter four genera, would appear to invalidate this distinction in being large-gaped fish with a forward angulo-articular-quadrate articulation. However, this seeming incongruity is a function of the autapomorphous manner in which the elongation of the jaws is achieved in these genera. Among other characoids the premaxilla extends little, if at all, anterior to the tip of the supraethmoid. Thus the effective gape is a function of the distance between the anterior margin of the supraethmoid and the articular condyle of the quadrate. In the distichodontid genera noted above, however, the elongation of the gape is a function of the lengthening of the premaxillae anterior to the supraethmoid. This adaptation together with the congruent changes in the supraethmoid, lower jaw and suspensorium permits an elongation of the gape despite the retention of an anterior position of the articulation between the angulo-articular and quadrate.

In addition to the above broad differences in overall suspensorium form, modifications of portions of this system characterize groups of varying levels of universality with the Distichodontidae. Two multigeneric assemblages within this family demonstrate a restructuring of the generalized characoid condition of a somewhat rectangular hyomandibula having a slightly concave anterior face. In *Nannocharax* and *Hemigrammocharax* the hyomandibula is markedly widened anteroposteriorly and has a relatively elongate articulation with the hyomandibular fossa (see Daget, 1961, Fig. 10). *Ichthyborus*, *Mesoborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in contrast, have an elongate hyomandibula with a deeply concave anterior margin (see Daget, 1967, Fig. 9). Both this form of hyomandibula and that occurring in the unit formed by *Hemigrammocharax* and *Nannocharax* appear to be derived characters serving to define these multigeneric units.

The hyomandibula exhibits several other modifications of note among distichodontids. In *Eugnatichthys* this bone has a dorsally-directed process arising from its dorsolateral border

(Fig. 16). A similar, although not as well-developed, process occurs in *Phago* and appears to be present in *Paraphago*. *Eugnatichthys* also possesses a medially-directed process on the medial surface of the hyomandibula. This structure both braces the bone against the ventral surface of the neurocranium and serves as a point of origin for portions of the *adductor mandibulae* muscles.

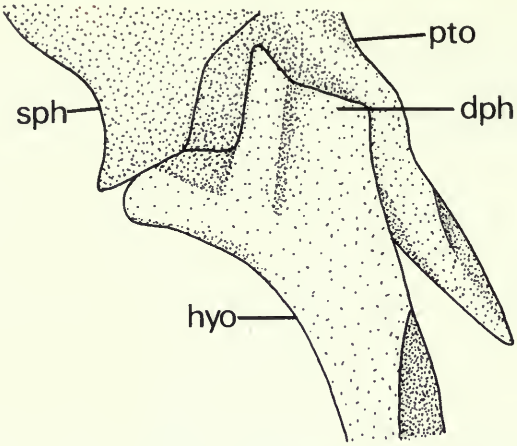

Fig. 16 *Eugnatichthys eetveldii*, posteroventral otic region and dorsal portion of the hyomandibula, left lateral view.

The final hyomandibular modifications of note among distichodontids involve the relationships of this element to the dorsal portion of the preopercle. Citharinids and distichodontids other than *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* retain the plesiomorphous characoid condition of a slight overlap of the lateral face of the vertical arm of the preopercle by the posterior border of the hyomandibula. In the listed genera, however, the posterior surface of the hyomandibula bears a vertically elongate depression just ventral to the articular condyle. This groove, which appears to be unique to these genera among characoids, tightly surrounds the dorsal tip of the preopercle (Fig. 17) and further reduces the possibility of motion between these elements.

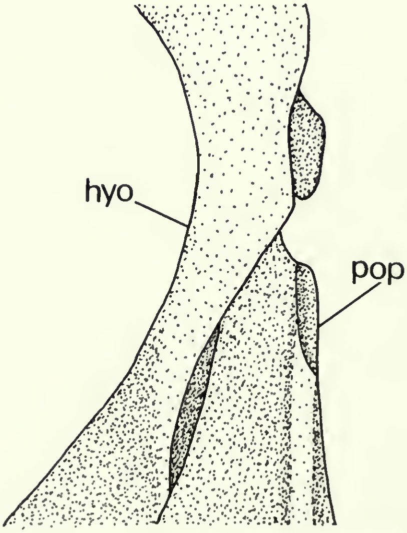

Fig. 17 *Phago loricatus*, central portion of the hyomandibula and posterodorsal section of the preopercle, left lateral view.

The preopercle, in turn, has undergone several modifications that distinguish groups of varying levels of universality within distichodontids. In *Hemistichodus*, *Ichthyborus*, *Microstomatichthyborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* the laterosensory canal segment in the vertical arm of the preopercle is shifted medially relative to the condition in citharinids and other distichodontids. This shift, which is especially pronounced in *Ichthyborus*, results in a broad separation of the laterosensory canal segment from the posterolateral edge of the bone. These genera, with the exception of *Ichthyborus* and *Hemistichodus*, are also characterized by the separation of the posterolateral portion of the preopercle as a distinct dorsally-directed process (Fig. 18). Both this lateral preopercular flange and the medial shift of the posterior portion of the preopercular laterosensory canal are hypothesized to be apomorphous characters.

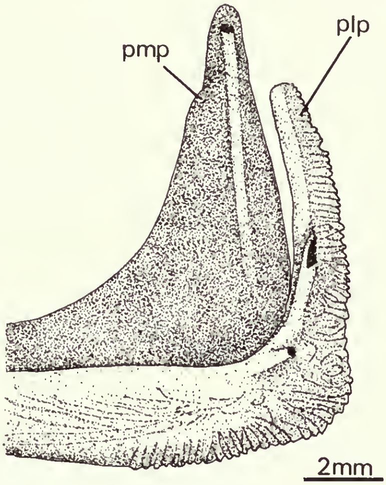

Fig. 18 *Phago loricatus*, posterior portion of the preopercle, left lateral view.

The final preopercular modification of note involves the development of a lateral preopercular shelf in some distichodontids. The lateral surface of the preopercle in citharinids and the distichodontid genera *Xenocharax*, *Nannaethiops* and *Neolebias* is nearly flat except for the slightly raised laterosensory canal. *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus*, in contrast, have a horizontal, laterally-directed ridge along the anterior portion of the preopercle. This lateral preopercular ridge is further elaborated, both posteriorly and laterally, in *Ichthyborus*, *Microstomatichthyborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* where it extends posteriorly to the vertical arm of the preopercle. In these genera these processes of the quadrate and preopercle form a distinct trough from which the expanded origin of the large A_1 and A_2 portions of the *adductor mandibulae* muscles partially arise. Such an elaboration of the preopercle and quadrate is hypothesized apomorphous for these genera, although occurring evidently independently in the South American characoid family Anostomidae.

The metapterygoid–quadrate fenestra undergoes a series of apomorphic alterations in various generic and multigeneric units among distichodontids. The plesiomorphous condition of the fenestra among characoids appears to be an horizontally ovoid opening bordered primarily by the metapterygoid dorsally and the quadrate ventrally, and with the symplectic forming a limited portion of its posteroventral border. A complete eradication of the fenestra occurs in *Neolebias spilotaenia* in which the enlarged symplectic fills the space primitively occupied by the fenestra. Correlated with the decreased vertical extent of the suspensorium in *Nannocharax* and *Hemigrammocharax* is a reduction or elimination of the fenestra as a consequence of the approximation of the quadrate and metapterygoid (see Daget, 1961, Fig. 10).

Hemistichodus, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in contrast, have a horizontally elongate metapterygoid–quadrate fenestra (see Daget, 1967, Fig. 9). In these genera the contribution of the symplectic to the border of the fenestra is greatly increased, with a congruent reduction of the portion of the border formed by the quadrate. Such seemingly apomorphous modifications are correlated with the lengthening of the metapterygoid and symplectic necessitated by the posterior shift of the hyomandibular fossa in these genera. This elongation of the fenestra is particularly pronounced in *Phago* and *Belonophago* in which the bones are exceptionally long and slender.

The final modifications of the suspensorium to be discussed involve the relationship of the anterior portion of the suspensorium to the upper jaw. The generalized characoid condition has a ligamentous or cartilaginous attachment of the palatine to the anteromedial maxillary process, and a loose ligamentous connection of the palatine to the vomerine region. In *Citharinus* and *Citharidium*, however, a large cartilage pad joins the palatine to the anteromedial process of the maxilla. Furthermore, citharinids have a second cartilaginous mass joining the palatine to the posterior surface of the premaxilla. Although a cartilaginous connection between the maxilla and palatine occurs in other characoid groups, both the size of the cartilage in citharinids, and the presence of a cartilaginous body between the palatine and premaxilla is unique to, and thus considered apomorphous for, these genera among the families under study.

Some species of *Nannocharax*, in contradistinction, have a partially ossified cartilaginous rod joining the palatine to the maxilla. Further study is necessary to determine whether this ontogenetically variable ossification, termed the submaxilla by Daget (1961), is a defining character for the genus or some subunit of it.

In distichodontids, other than *Xenocharax*, *Nannaethiops*, *Neolebias* and *Paradistichodus*, the mesopterygoid is more tightly joined to the lateral ethmoid than in the hypothesized plesiomorphous condition. Furthermore, the palatine in these genera is distinctly more enveloped by the ectopterygoid and mesopterygoid than in the generalized state. This trend is most pronounced in *Ichthyborus* and the unit formed by *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* which have a reduced palatine fitting into a depression along the dorsal surface of the ectopterygoid and lacking the plesiomorphous ligamentous attachment to the maxilla.

Finally, it should be noted that the quadrate and palatine have been found to be separate in all *Paradistichodus* specimens examined, contrary to Daget (1968, Fig. 10) who illustrated these elements are fused.

In summary, derived characters in the suspensorium of the citharinids and distichodontids are:

1. the anterior position of the articulation of the angulo-articular and quadrate in all distichodontids other than *Xenocharax*, *Neolebias* and *Nannaethiops*.
2. the broadened hyomandibula in *Hemigrammocharax* and *Nannocharax*.
3. the slender, anteriorly concave hyomandibula in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
4. the dorsolateral and dorsomedial hyomandibular processes present in various distichodontids.
5. the groove on the posterior surface of the hyomandibula in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
6. the lateral horizontal preopercular shelf in all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*. This shelf is most distinctly developed, both posteriorly and laterally, in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
7. the medial shift of the laterosensory canal segment in the vertical arm of the preopercle in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This assemblage, with the exception of *Ichthyborus*, is also characterized by the development laterally of a distinct posterodorsal preopercular flange.
8. the reduction or loss of the metapterygoid–quadrate fenestra in *Neolebias spilotaenia* and the unit formed by *Nannocharax* and *Hemigrammocharax*.
9. the elongate metapterygoid–quadrate fenestra of *Ichthyborus*, *Mesoborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

10 the two large cartilage pads between the palatine and upper jaw of citharinids.
11 the increased attachment of the palatine and mesopterygoid to the neurocranium in distichodontids other than *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus*.
12 the loss of the ligamentous connection between the palatine and the maxilla in *Ichthyborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Opercle

On the basis of outgroup comparisons, the plesiomorphous form of the opercle among characoids is hypothesized to be a flat and unfenestrated bone. Such an opercular form occurs in the distichodontid genus *Xenocharax*, but is variously modified in citharinids and all other distichodontids.

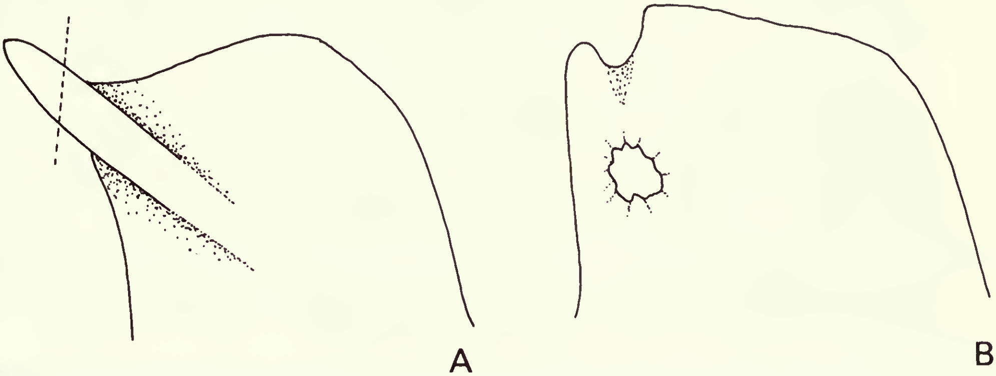

Fig. 19 Dorsal portion of the opercle of A. *Citharinus citharus* (dotted line denotes position of the suprapreopercle), B. *Distichodus notospilus*, left lateral view.

Laterally the opercle of *Citharinus* and *Citharidium* bears a prominent, anterodorsally oriented ridge aligned at an acute angle relative to the anterior border of the opercle (Fig. 19a). This ridge extends dorsally from the body of the opercle to the tip of the elongate anterodorsal corner of the bone. Such a lateral opercular ridge has not been encountered elsewhere among charcoids except in the Neotropical characoid family Curimatidae (Roberts, 1974). The opercular flange of curimatids differs, however, from that of citharinids in its less extensive vertical development, and in not extending to the anterodorsal edge of the bone.

Among distichodontids other than *Xenocharax*, the opercle undergoes a progressive fenestration. The simplest condition of this opening occurs in *Nannaethiops* and *Neolebias* which have a series of small, closely apposed holes extending through the opercle. These foramina, which are located slightly posterior to the facet for articulation with the hyomandibula, appear to be the precursors of the distinct opercular fenestra occupying this region in the remaining distichodontids with the exception of *Xenocharax* (Fig. 19b). As far as can be determined, neither this distinct fenestra nor the series of small openings in *Nannaethiops* and *Neolebias* serve for the passage of any nerves, blood vessels or muscle fibres. In *Hemigrammocharax* and *Nannocharax* the opercle is reduced dorsally with a consequent opening of the opercular fenestra to the dorsal margin of the bone. The resultant vertical slit separates the anterodorsal portion of the opercle, to which the *dilator operculi* muscles attach, from the posterodorsal plate-like portion of the bone. None of these forms of fenestrated opercle have been encountered elsewhere in characoids, or among the non-characoid ostariophysans examined. Consequently, these modifications are considered to represent apomorphous characters of varying levels of universality.

In summary, the hypothesized derived opercular characters among citharinids and distichodontids are:

1 the prominent lateral opercular ridge in citharinids.

2 the fenestrated opercle in all distichodontids other than *Xenocharax*. Three increasingly apomorphous forms of the opening occur in these genera:
(A) the series of small holes in *Nannaethiops* and *Neolebias*.
(B) the distinct fenestra of all distichodontids other than *Nannaethiops*, *Neolebias* and *Xenocharax*.
(C) the vertical slit along the dorsal margin of the opercle in *Nannocharax* and *Hemigrammocharax*.

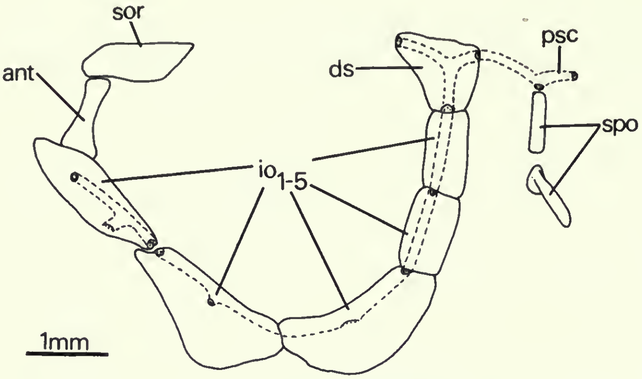

Fig. 20 *Xenocharax spilurus*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

Dermosphenotic, pterotic and suprapreopercle

The general morphological diversity of the family Citharinidae and Distichodontidae is reflected in the overall structure and in the patterns of the sensory canals of the dermosphenotic, pterotic and suprapreopercle. Prior to a discussion of these characters, however, it is necessary to comment on the nomenclature of some of the sensory canal-bearing bones of the lateral edge of the skull. Daget, in a series of publications (1958–1968), distinguished the canal-bearing dermosphenotics and dermopterotics from the underlying sphenotics and pterotics. Similarly, Gregory (1933) and Gregory & Conrad (1938) illustrate a separate dermosphenotic in *Distichodus langi*, *Mesoborus* and *Phago*, and distinguish the scale bone (the dermopterotic of Daget) from the underlying pterotic.

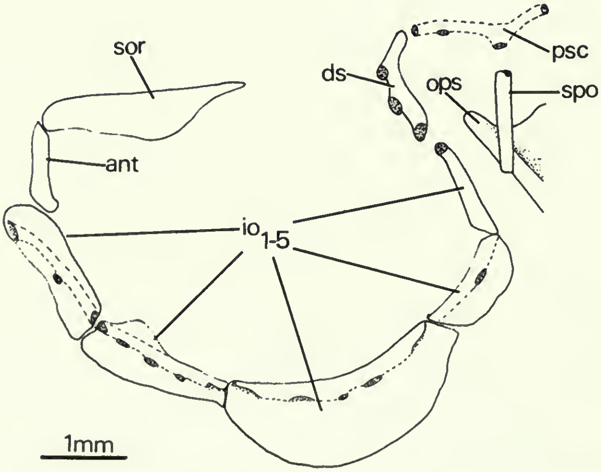

Fig. 21 *Citharidium ansorgei*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

When present the dermosphenotic (or infraorbital 6) of characoids is independent throughout ontogeny from the underlying sphenotic. In light of such a separation, this element should obviously be recognized as a distinct bone, the dermosphenotic. However, in none of the characoids examined are the pterotic (*sensu stricto*) and the lateral canal-bearing element (Daget's dermopterotic and Gregory & Conrad's scale bone) separate elements. Neither has such a separation been reported in the literature for any adult characoid. Indeed, a separate dermopterotic is rare among teleosts (Patterson, 1977, p. 97). Although these elements arise independently from cartilaginous and intramembranous elements (Weitzman, 1962, p. 25) they fuse early in ontogeny and I will follow Weitzman in considering the resultant bone as a single unit, the pterotic. The pterotic in this sense is equivalent to the pterotic plus scale bone of Gregory & Conrad, and the pterotic plus dermopterotic of Daget.

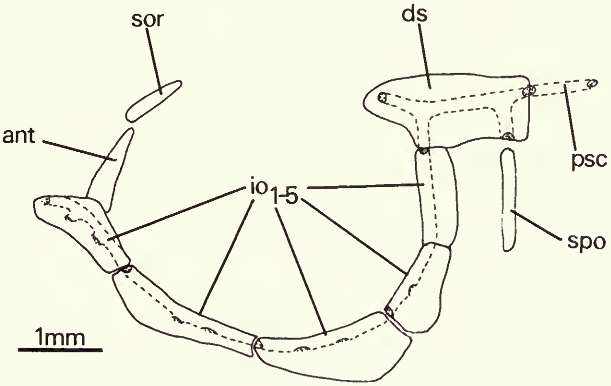

Fig. 22 *Paradistichodus dimidiatus*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

Within the families Citharinidae and Distichodontidae four main patterns of the dermosphenotic and pterotic and of their relationships to the infraorbitals and supraperopercle can be discerned. On the basis of outgroup comparisons, the plesiomorphous form of these bones and the associated canals among characoids appears to be similar to that of *Xenocharax* (Fig. 20). The moderately sized dermosphenotic completely roofs over the dilatator fossa and carries a Y-shaped segment of the laterosensory canal system. The ventral segment of the dermosphenotic sensory canal communicates with that of the fifth infraorbital, the anterior branch with the supraorbital sensory canal of the frontal and the posterodorsal section with the pterotic sensory canal. The pterotic, in turn, is broadly exposed laterally and bears a trifurcate sensory canal system. The anterior branch of the pterotic sensory canal contacts the posterior portion of the dermosphenotic sensory canal, the posterior segment communicates with the extrascapular sensory canal, and the ventral branch receives the preopercular sensory canal by way of the suprapreopercle.

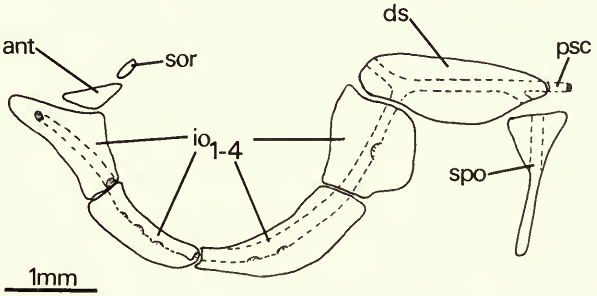

Fig. 23 *Ichthyborus besse*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

The remaining genera in the families Citharinidae and Distichodontidae exhibit a series of apomorphous modifications of the above plan of these bones and sensory canals. *Citharinus* and *Citharidium*, although retaining the plesiomorphous sensory canal pattern, have greatly reduced the dermosphenotic into a tube-like element which no longer contacts the edges of the dilatator fossa and only partially covers the lateral surface of the *dilatator operculi* muscle (Fig. 21). In contradistinction, in all distichodontids other than *Xenocharax*, the dermosphenotic, when present, is posteriorly expanded relative to the hypothesized plesiomorphous condition. As a consequence of this expansion, the dermosphenotic overlaps much of the primitively exposed lateral surface of the pterotic and separates the suprapreopercle from its direct contact with the pterotic laterosensory canal system (see below with respect to *Nannaethiops* and *Neolebias*).

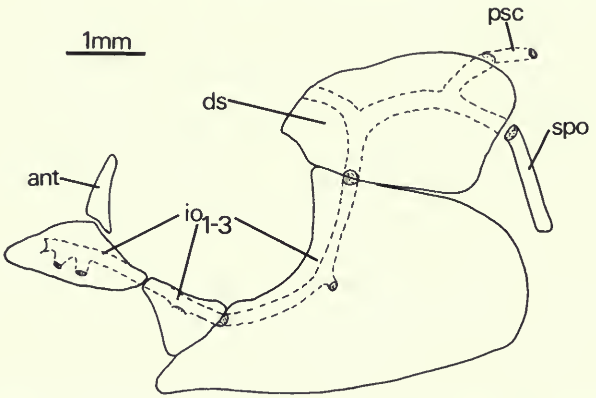

Fig. 24 *Phago intermedius*, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

This shift of the contact of the suprapreopercle and the expansion of the dermosphenotic results in a marked change in the sensory canal system in these bones. Whereas the dermosphenotic sensory canal is bifurcate anteriorly as in *Xenocharax*, the posterior branch of the canal is drawn out along the horizontally elongate dermosphenotic and bifurcates posteriorly (Figs 22, 23, 24). As a consequence the posteroventral branch of the canal contacts the dorsal tip of the suprapreopercle while the posterodorsal segment communicates with the pterotic sensory canal. This expansion of the dermosphenotic sensory canal results in a horizontally elongate, somewhat H-shaped system. Outgroup comparisons among characoids have failed to reveal a comparable posterior expansion of the dermosphenotic. Neither have there been discovered any other characoids in which the dermosphenotic directly communicates both with the infraorbital and preopercular sensory canal systems. Furthermore, the reduced lateral exposure of the pterotic and the shift in the contact of the suprapreopercle has resulted in a pronounced reduction of the pterotic sensory canal segment. Rather than the plesiomorphous Y-shaped system of most characoids, in these genera the pterotic laterosensory canal is a simple, short tube joining the dermosphenotic and the extrascapular sensory canals. Such a reduction is particularly pronounced in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* in which the laterally exposed portion of the pterotic is a small wedge of bone between the rear of the dermosphenotic and the margin of the extrascapular.

Autapomorphous modifications of the above form of dermosphenotic and of the associated laterosensory canals characterize several subunits of the assemblage having this pattern of these bones. In *Ichthyborus* the dermosphenotic is shifted posterodorsally and thus is totally removed from the orbital rim. This shift, along with the dorsal elongation of the suprapreopercle in this genus, is reflected in the posteroventral reduction of the dermosphenotic and in the shortening of the posterodorsal and posteroventral portions of the dermosphenotic sensory canal system (Fig. 23). In *Paraphago*, in contrast, the dermosphenotic is somewhat expanded ventrally. This expansion is a precursor of the markedly expanded dermosphenotic in *Phago* and *Belonophago* where the large plate-like bone extends ventrally midway along the posterior rim of the orbit (Fig. 24). The enlarged dermosphenotic of *Belonophago* is autapomorphously further modified by the total loss of its sensory canal system.

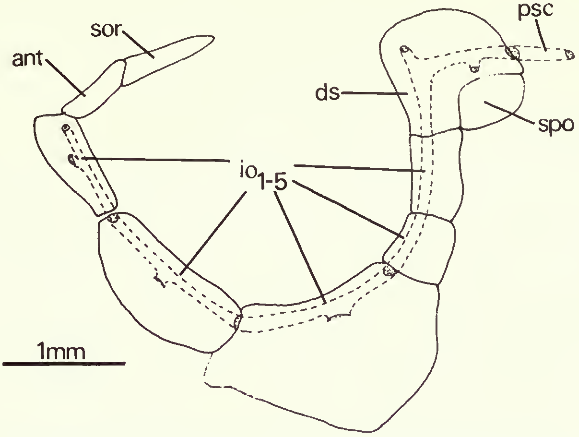

Fig. 25 *Nannaethiops unitaeniatus*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

The monophyletic unit formed by *Nannaethiops* and *Neolebias* is characterized by a progressive apomorphic reduction of the dermosphenotic and pterotic sensory canals common to distichodontids other than *Xenocharax*. The least pronounced reduction is found in *Nannaethiops unitaeniatus* (Fig. 25) which has a slight shortening of the posteroventral branch of the dermosphenotic sensory canal. The reduction of this canal segment, which primitively communicates with the suprapreopercle, is congruent with the loss of the suprapreopercular sensory canal in *Nannaethiops* and *Neolebias* (see discussion on the suprapreopercle). The dermosphenotic, pterotic and their sensory canals in *Neolebias unifasciatus* (see Daget, 1965, Fig. 7) and *N. trewavasae* are similar to that of *Nannaethiops* other than for the pronounced reduction or loss of the anterodorsal and posterodorsal branches of the dermosphenotic sensory canal system. Apomorphic reduction of the dermosphenotic laterosensory canals is further advanced in *N. trilineatus*, *N. bidentatus* and *N. axelrodi* where the sensory canals of the dermosphenotic and pterotic are totally lacking. This reductional trend reaches its terminal stage in *N. spilotaenia* in which the dermosphenotic is lost, together with that portion of the pterotic which plesiomorphously carries the pterotic sensory canal segment. These progressive reductions of the dermosphenotic sensory canals and the eventual loss of the bone itself are considered to be a series of derived characters of decreasing levels of universality (see the Phylogenetic analysis).

The marked modifications of the dermosphenotic and pterotic described above appear to have resulted in several misinterpretations of distichodontid skull osteology by Gregory & Conrad. In their figure of the skull of *Phago* (1938, Fig. 35) those authors illustrate the dermosphenotic and pterotic as part of a single ossification. The bone indicated is, however, the dermosphenotic which almost totally overlaps the pterotic in this genus. The exposed portion of the pterotic is actually the small scale bone of those workers. The same authors in their drawing of the skull of *Mesoborus* (1938, Fig. 34), show an unlabelled dermosphenotic which incorporates the sensory canals of the pterotic and extrascapular along its posterodorsal margin. Examination of this species, however, shows that these sensory canals are actually separate tubes in their respective bones.

In the course of the above discussion, it was noted that the preopercular sensory canal of citharinids and distichodontids communicates with the sensory canal system of the pterotic or expanded dermosphenotic by way of an ossified suprapreopercle. Such a canal-bearing suprapreopercle or a derived form of the bone is common to all citharinids and distichodontids other than some *Neolebias* species in which it is hypothesized to be secondarily lost (see below). The possession of a suprapreopercle would appear apomorphous in characoids although occurring in a variety of ostariophysan groups. Despite the uncertainty on the exact distribution of this element and on the interrelationships of the groups possessing it, at the least, the common possession of this element is congruent with the hypothesized monophyletic nature of the unit formed by the families Citharinidae and Distichodontidae. In its simplest form the suprapreopercle is a bony tube extending from the dorsal opening of the preopercular sensory canal to the sensory canal system of the pterotic or dermosphenotic. Such a suprapreopercular form, which represents an ossification of the primitively unossified tube joining these systems, is modified in the Citharinidae and subunits of the Distichodontidae.

In *Citharinus* and *Citharidium* the elongate tube-like suprapreopercle extends over the lateral surface of the anterodorsal corner of the opercle (Fig. 21). Such a transversing of the opercle by the suprapreopercle has not been encountered elsewhere among characoids examined and thus appears autapomorphous for these genera. Among distichodontids the plesiomorphous tubular suprapreopercle is modified in several distinctive apomorphous modes. The simplest of these adaptations occurs in *Ichthyborus besse* where the suprapreopercle bears anterodorsal and posterodorsal flanges that give it a somewhat triangular form (Fig. 23). In *Xenocharax*, in contrast, the suprapreopercle retains its basically tubular shape, but is subdivided horizontally into two short tubes (Fig. 20). The remaining and most radical restructuring of the suprapreopercle occurs in *Nannaethiops* and *Neolebias*. As illustrated in Fig. 25 for *Nannaethiops unitaeniatus* these genera have an independent ossification fitting the posteroventrally concave border of the dermosphenotic (see also Daget, 1965, Fig. 7). Although it carries no sensory canal segment, this independent ossification is hypothesized to represent a highly modified suprapreopercle. Such an hypothesis is congruent with its location in the region primitively occupied by the plesiomorphous tubular suprapreopercle. Furthermore, this element contacts the posteroventral dermosphenotic sensory canal segment which plesiomorphously communicates with the suprapreopercle. In light of this association and the relative position of the element, it is most parsimonious to assume that this plate-like, non-canal-bearing element is homologous with the tubular suprapreopercle of citharinids and other distichodontids. This flattened suprapreopercle is lost, evidently secondarily, in *Neolebias spilotaenia* which is characterized by an extreme reduction of various dermal elements of the skull.

Daget, in his illustration of *Neolebias unifasciatus* (1965, Fig. 7), identified the element herein considered the suprapreopercle as an infraorbital (the postorbital of Daget). It would appear that Daget believed this bone to be a posteriorly shifted fourth or fifth infraorbital. Such an homology would give a full series of five infraorbitals plus the dermosphenotic for the species. However, the identification of this independent ossification as an infraorbital appears erroneous if we examine the infraorbital series of *Neolebias trewavasae* and *Nannaethiops unitaeniatus* (Fig. 25). These species, which have the infraorbital reductional trends characteristic of these genera least pronounced, retain a full series of infraorbitals in addition to the independent ossification termed an infraorbital by Daget. In light of this condition and the previously discussed information indicating that the independent ossification is a modified suprapreopercle, the identification of the element as an infraorbital is herein considered incorrect.

Hypothesized apomorphic states of the dermosphenotic, pterotic, suprapreopercle and their associated sensory canals among citharinids and distichodintids are:

1 the reduced tubular dermosphenotic of citharinids.
2 the posterior expansion of the dermosphenotic in all distichodontids other than *Xenocharax*. These genera have a congruent reduction of the laterally exposed portion of the pterotic and a shift of the contact of the suprapreopercular sensory canal to the dermosphenotic.
3 the posterodorsal shift of the dermosphenotic in *Ichthyborus*.
4 the ventral expansion of the dermosphenotic in *Paraphago*, *Phago* and *Belonophago*. This expansion is particularly pronounced in the last two genera.
5 the loss of the dermosphenotic sensory canal system in *Belonophago*.

6 the progressive reduction of the dermosphenotic and pterotic sensory canal systems in *Nannaethiops* and *Neolebias*.
7 the suprapreopercle common to citharinids and distichodontids.
8 the subdivision of the suprapreopercle in *Xenocharax*.
9 the extension of the suprapreopercle across the opercle in citharinids.
10 the modification of the dermosphenotic into a flat, non-canal-bearing plate in *Neolebias* and *Nannaethiops*.

Supraorbital and infraorbitals

The hypothetical plesiomorphous infraorbital series for characoids consists of a chain of six canal-bearing bones (a dermosphenotic and five infraorbitals) which, together with the supraorbital, form a bony rim to the orbit. The modifications of the dermosphenotic (infraorbital 6) and its associated sensory canals were discussed in the previous section. Reductions, expansions and losses of the supraorbital, infraorbitals 1 to 5 and the infraorbital sensory canal system characterize subunits of varying levels of universality among distichodontids.

A large supraorbital forming the anterodorsal portion of the orbital rim is common to *Citharinus* and *Citharidium* (Fig. 21). Although somewhat enlarged relative to that of many characoids, the citharinid form of supraorbital nonetheless appears to be plesiomorphous among citharinids and distichodontids in forming a large portion of the anterodorsal rim of the orbit and in extending beyond the posterior margin of the lateral ethmoid. The distichodontid genera *Xenocharax* (Fig. 20), *Nannaethiops*, *Neolebias*, *Paradistichodus* (Fig. 22), *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus* and *Ichthyborus* (Fig. 23) differ from citharinids and the generalized characoid condition in having an anteriorly shifted supraorbital which is variously reduced. The remaining distichodontid genera, in turn, have the supraorbital totally lacking, a loss that is considered apomorphous within distichodontids (in *Neolebias spilotaenia*, a supraorbital ossification was found only in the largest specimens examined). Although David & Poll's illustration (1937, Fig. 9) of the jaws and dermal bones of the anterior portion of the head of *Microstomatichthyoborus bashforddeani* and *M. katangae* includes a prominent 'supraorbital', examination of these species has shown that those 'supraorbitals' are actually the antorbitals.

Subunits of the Distichodontidae also differ in the total number of infraorbitals, their relative sizes and the extent of the infraorbital sensory canal system. Three different types of reduction from a full series of five canal-bearing infraorbitals are discernable in different subunits of the family (see the previous section for a discussion of the variation in the dermosphenotic, infraorbital 6). Two of these reductions result in a partially unossified orbital rim, while the third retains a continuous infraorbital series.

The first of these modifications to be discussed is the progressive reduction of the infraorbital series within the genus *Neolebias*. *Neolebias trewavasae* has a full series of five infraorbitals, with two elements (infraorbitals 4 and 5) forming the posterior rim of the orbit. In *N. unifasciatus* and *N. bidentatus*, in contrast, there is only a single infraorbital at the rear of the orbit, with the remaining elements shifted so as to retain a fully ossified orbital rim (see Daget, 1965, Fig. 7). The remaining infraorbital at the posterior margin of the orbit is lost in *N. trilineatus*, *N. ansorgei*, *N. axelrodi* and *N. spilotaenia* in which the posterior orbital border is unossified. This reductional trend reaches its terminal stage in *N. spilotaenia* which additionally lacks infraorbitals 2 and 3 and the sensory canal segment in infraorbital 1. The progressive reduction of the infraorbital series from a chain of five canal-bearing elements to a single non-canal-bearing bone is considered to represent a series of derived reductional characters of varying levels of universality, and is congruent with the overall reduction of the dermal skull elements in these genera.

The second reduction of the infraorbital series among distichodontids occurs in *Nannocharax* and *Hemigrammocharax*. In *Nannocharax multifasciatus*, *N. fasciatus* (Daget, 1961, Fig. 7) and *Hemigrammocharax wittei* the fourth and fifth infraorbitals are reduced to two bony tubes dorsal to an expanded third infraorbital. In contrast, the specimens of *Nannocharax niloticus*, *N. ansorgei*, *N. gobioides*, *N. intermedius*, *Hemigrammocharax machadoi* and *H. polli* examined have infraorbitals 4 and 5 totally lacking. Although this reduction results in an unossified posterior orbital border similar to that in some *Neolebias* species, the phylogenetic sequence of the reductions and losses leading up to this condition differ significantly from that in *Neolebias*. Consequently, the unossified posterior orbital rim in the listed *Nannocharax* and *Hemigrammocharax* species and that of the previously noted *Neolebias* species are considered to be non-homologous.

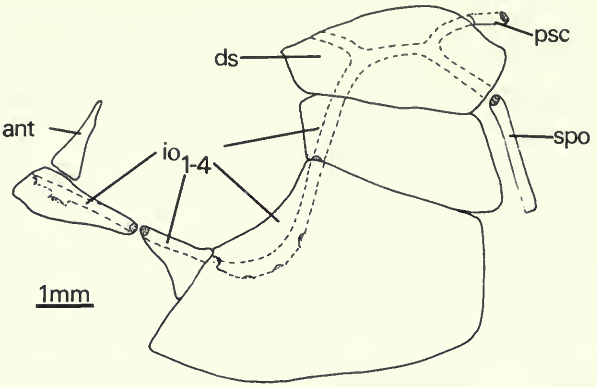

Fig. 26 *Eugnatichthys eetveldii*, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

The final reductional transition series of the infraorbitals among distichodontids occurs within the assemblage consisting of *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Contrary to the hypothesized plesiomorphous condition of an infraorbital series with five elements, these genera are characterized by a maximum of four infraorbitals. This reduced infraorbital count appears to be a consequence of the loss of an infraorbital at the posterior margin of the orbit. The exact homology of the remaining element, that is whether it represents the plesiomorphous infraorbital 4, infraorbital 5 or a fusion of these bones, is uncertain. However, for simplicity in the following discussion the bone is arbitrarily termed infraorbital 4. Within this assemblage, *Ichthyborus* (Fig. 23) has a relatively narrow infraorbital series, but with infraorbital 4 expanded posterodorsally so as to separate distinctly the dermosphenotic from the orbital rim. In contrast, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys* (Fig. 26), *Paraphago*, *Phago* (Fig. 24) and *Belonophago* have the posterior infraorbital elements widened, with infraorbital 3 expanded posteriorly so as to cover a major portion of the cheek. Anteroventrally infraorbital 3 is produced into a distinct process extending ventral to infraorbital 2 and almost to the vertical through the articular condyle of the quadrate. Within this assemblage *Paraphago* has the fourth infraorbital reduced to a narrow, horizontally elongate element and it is completely lacking in *Phago* (Fig. 24) and *Belonophago*. As a consequence of these changes the enlarged third infraorbital of *Phago* and *Belonophago* completely covers the cheek and is in direct contact dorsally with the expanded dermosphenotic. Among members of these families, the enlarged third infraorbital in *Belonophago* is also unique in its total lack of a sensory canal segment. The loss of infraorbitals 4 and 5 in these genera differs from that among the previously described *Neolebias*, *Nannocharax* and *Hemigrammocharax* species in that the expansion of the remaining infraorbitals fills the space primitively occupied by the missing elements, and a fully ossified orbital rim is thus retained.

Two differences between the observations of this study and those of Gregory & Conrad (1938) and Daget (1968) should be noted. In their illustration of the skull of *Mesoborus*, Gregory & Conrad (1938, Fig. 34) show a single infraorbital (the suborbital of those authors) in the region plesiomorphously occupied by infraorbitals 1 and 2. However, examination of the specimen probably illustrated by those workers, along with other *Mesoborus* material, shows there to be two distinct infraorbitals preceding the expanded infraorbital 3. Similarly, Daget (1968, Fig. 4) in his illustration of the skull of *Hemistichodus vaillanti* shows a single large infraorbital in the region normally occupied by infraorbitals 2 and 3. However, all specimens of the three nominal *Hemistichodus* species examined have the second and third infraorbitals as separate elements.

In summary, hypothesized apomorphous supraorbital and infraorbital characters among distichodontids are:

1 the reduction and anterior shift of the supraorbital in *Xenocharax*, *Nannaethiops*, *Neolebias*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Ichthyborus*. This reduction is a precursor of the further apomorphous loss of the element in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
2 the reduction to a single infraorbital at the rear of the orbit in *Neolebias unifasciatus* and *N. bidentatus*, with the remaining element lost in *N. trilineatus*, *N. ansorgei*, *N. axelrodi* and *N. spilotaenia*.
3 the loss of infraorbitals 2 and 3 and the sensory canal of infraorbital 1 in *N. spilotaenia*.
4 the reduction of infraorbitals 4 and 5 to bony tubes or a loss of these elements in *Nannocharax* and *Hemigrammocharax*.
5 the loss of infraorbital 5 in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
6 the expansion of infraorbital 4 to exclude the dermosphenotic from the orbital rim in *Ichthyborus*.
7 the reduction of infraorbital 4 in *Paraphago* and its loss in *Phago* and *Belonophago*.
8 the loss of the sensory canal segment of infraorbital 3 in *Belonophago*.
9 the anterior and posterior expansion of infraorbital 3 in *Microstomatichthyoborus*, *Eugnatichthys*, *Mesoborus*, *Paraphago*, *Phago* and *Belonophago*.

Branchial apparatus

The morphology of the branchial apparatus among members of the families Citharinidae and Distichodontidae demonstrates a significant degree of variation for a system that is otherwise rather stable among characoids. Major branchial apparatus modifications occur in *Citharinus* and *Citharidium*, whereas less pronounced adaptations distinguish various distichodontid subunits.

The fifth ceratobranchial (lower pharyngeal) of citharinids is highly modified with respect to the relatively flat, anteromedially tooth-bearing elements common to most characoids. In *Citharinus* and *Citharidium* the medial portion of the fifth ceratobranchial is a dorsally bulbous, highly fenestrated structure bearing only a few greatly reduced, loosely attached teeth (Fig. 27). These genera also demonstrate a comparable reduction and modification of the upper pharyngeal tooth plates and their associated dentition. Among most characoids, the fourth epibranchial and cartilaginous fourth pharyngobranchial articulate with the tooth-bearing fourth and fifth upper pharyngeal tooth plates respectively (see Rosen, 1973, Fig. 3). In contradistinction, citharinids either have the upper pharyngeal dentition totally lacking or reduced to a few loosely-attached minute spicules. More significantly, the fourth and fifth upper pharyngeal tooth plates of citharinids are fused to form an elongate bony plate (Fig. 28). Such a distinctive upper pharyngeal ossification has not been encountered elsewhere among characoids and would appear to be apomorphous, as is its edentulous nature. Similarly, the highly modified lower pharyngeals of *Citharinus* and *Citharidium* are, as best as can be determined, autapomorphous for these genera among characoids. Further apomorphic characters in the branchial apparatus of citharinids include their loss of the first pharyngobranchial and the elongation and reorientation of the second and third pharyngobranchials. These alterations result in a close approximation of the tips of the first epibranchial and the second and third pharyngobranchials.

The marked restructuring of the branchial apparatus among citharinids would seem to be an adaptation to their filter-feeding mode of life. An additional gill arch character congruent with this feeding method is the presence of micro-gillrakers in all citharinids. Micro-gillrakers are a series of parallel bands of small, bony spicules located along both faces of the gill arch between the gillrakers and gill filaments (Gosse, 1956; Daget, 1962). On the basis of our present knowledge on micro-gillraker distribution, it appears that these structures are unique to citharinids among characoids.

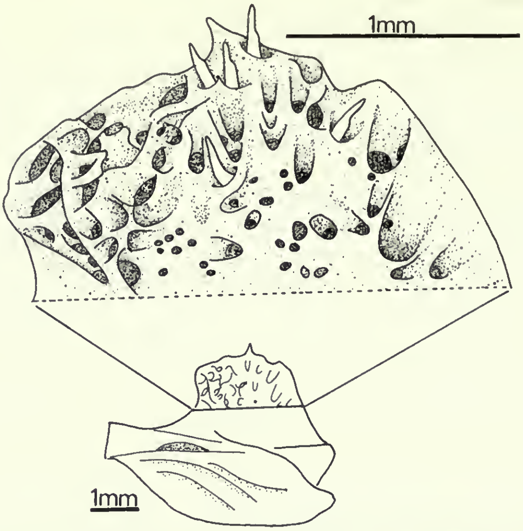

Fig. 27 *Citharidium ansorgei*, fifth ceratobranchial, right side, medial portion enlarged, dorsal view.

Alterations of the branchial apparatus among distichodontids are not as radical as those in citharinids and are primarily reductional. In most *Neolebias* species the fourth upper pharyngeal tooth plate is slightly ossified, with this element and its associated dentition totally lacking in *N.* spilotaenia (Fig. 29). Furthermore, in *N. spilotaenia* the fifth upper pharyngeal tooth plate is a reduced rounded ossification bearing approximately only six teeth. Similarly, the tooth-bearing portion of the lower pharyngeals is reduced to a small ovoid patch with a correlated reduction in the number of teeth.

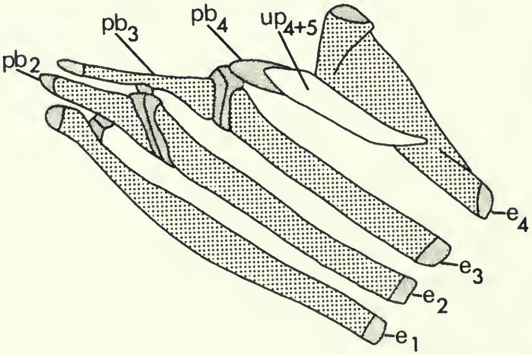

Fig. 28 *Citharidium ansorgei*, gill arches, dorsal parts of right side, ventral view.

An ossified fourth upper pharyngeal tooth plate and its associated dentition is also lacking in *Hemigrammocharax machadoi*, *Nannocharax fasciatus* and *N. niloticus*. However, based on the most parsimonious reconstruction of the phylogeny of citharinids and distichodontids, this loss is considered to have occurred independently of that in *Neolebias*. Furthermore, it is noteworthy that the lack of a fourth upper pharyngeal tooth plate is not universal within *Nannocharax*. *Nannocharax intermedius* has a small, slightly ossified fourth upper pharyngeal tooth plate, whereas *N. gobioides* and *N. ansorgei* have a larger but still reduced form of the bone. The resolution of the question of whether this variation in the extent of the ossification of this element represents a phylogenetic reductional trend within the genus or whether it is a function of ontogenetic variation awaits further study.

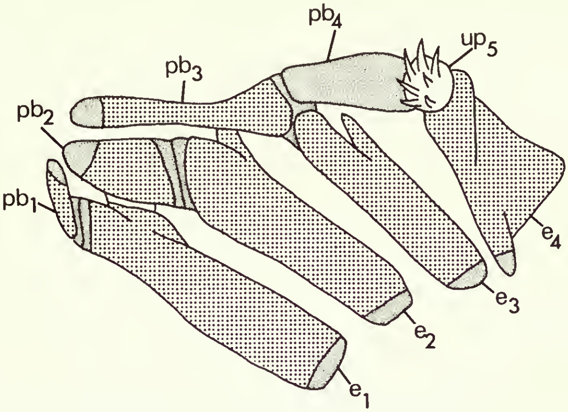

Fig. 29 *Neolebias spilotaenia*, gill arches, dorsal parts of right side, ventral view.

Among the remaining distichodontid genera no alterations of branchial apparatus structure have been found. However, congruent with their restructured neurocranial form, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have a posterior shift in the attachment of the suspensory pharyngeals to the neurocranium. Within this assemblage *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have an additional shift of this attachment ventrally, a trend that is most pronounced in the latter four genera where the pharyngeal attachment is to the previously described median parasphenoid ridge. It would appear that these shifts of gill arch attachment in these genera are a function of the extension of the *adductor mandibulae* muscle onto the medial surface of the hyomandibula and its expansion into regions plesiomorphously occupied by the branchial apparatus.

In summary, hypothesized derived states of the branchial apparatus among citharinids and distichodontids are:

1. the highly fenestrated, dorsally bulbous, nearly edentulous lower pharyngeal in citharinids.
2. the fusion of the fourth and fifth upper pharyngeal tooth plates in citharinids.
3. the loss of the first pharyngobranchial and the anterior elongation of the second and third pharyngobranchials in citharinids.
4. the loss of the fourth upper pharyngeal tooth plate and its associated dentition in *Neolebias spilotaenia*. This species also demonstrates a reduction of the fifth upper pharyngeal tooth plate and of the dentition associated with that element and the fifth ceratobranchial.
5. the micro-gillrakers in citharinids.
6. the reduction or loss of the fourth upper pharyngeal tooth plate in various *Nannocharax* and *Hemigrammocharax* species.
7. the posterior shift of the attachment of the suspensory pharyngeals in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
8. the ventral shift of the suspensory pharyngeals onto the median parasphenoid ridge in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Weberian apparatus

The common possession of the Weberian apparatus, an otophysic connection between the anterior chamber of the swimbladder and the middle ear, characterizes the series Otophysi of the superorder Ostariophysi (Rosen & Greenwood, 1970). The Weberian apparatus is composed of the Weberian ossicles (the pars auditum) and their supporting vertebrae (the pars sustentaculum). The Weberian ossicles are four small bones, the tripus, intercalarium, scaphium and claustram (the intercalarium and claustrum are lacking in some groups), that are joined by ligamentous bands and pivot on the anterior vertebrae. It is believed that vibrations induced in the anterior chamber of the swimbladder by soundwaves in the surrounding medium are transmitted by these ossicles to the middle ear, thereby aiding in sound reception (see Alexander, 1966, for a discussion of the mechanism). The pars sustentaculum is derived from the four or more anterior vertebrae and serves as a base for the Weberian ossicles and the shortened first pleural rib. In the generalized characoid condition the vertebrae of the pars sustentaculum are ventrally unfused and unmodified, with the fourth vertebrae bearing a pair of shortened, modified pleural ribs. Arising from the medial surface of each of these ribs is a distinct process, the os suspensorium, which serves for the support and attachment of the peritoneal layer of the anterior swimbladder chamber. The dorsal aorta, which is in contact with the ventral surface of these vertebrae, is surrounded laterally and to varying degrees ventrally by the shortened first pleural rib and os suspensorium.

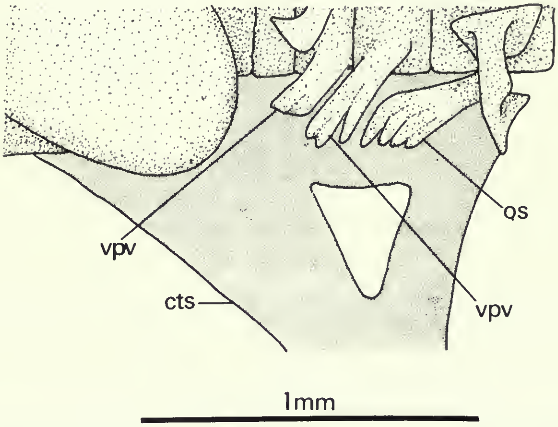

Fig. 30 *Nannaethiops unitaeniatus*, posteroventral section of neurocranium, ventral portion of pars sustentaculum and connective tissue sheath, left lateral view, Weberian ossicles removed.

All characoids examined have a triangular connective tissue system associated with the pars sustentaculum, the anterior section of the coeliac artery and the peritoneal covering of the anterior chamber of the swimbladder. This complex (Fig. 30) arises anterodorsally from the parasphenoid and basioccipital and posterodorsally from the os suspensorium. Dorsally it encompasses the dorsal aorta and anteriorly surrounds the anterior portion of the coeliac artery. The posterior section of this complex is formed by a medial thickening in the peritoneal covering over the anterior swimbladder chamber. This connective tissue band extends from the os suspensorium to the point of contact of the coeliac artery with the anterodorsal surface of the swimbladder chamber. Alexander (1962) applied the term 'coeliac sheath' to that portion of the system encompassing the coeliac artery in the Neotropical characoid genus *Leporinus*. In the following discussion, however, the term sheath is applied to the entire complex, unless a specific section (e.g. coeliac sheath) is cited.

Although the Weberian apparatus, particularly portions of the pars sustentaculum, undergoes pronounced restructuring in various ostariophysan groups (see Alexander, 1962, 1964*a*, 1964*b*) it has been traditionally considered morphologically conservative among characoids. However, an examination of the Weberian apparatus in the families Citharinidae and Distichodontidae has revealed a series of modifications of the pars sustentaculum, os suspensorium and of their relationships to the connective tissue sheath. Four major types of modifications to this complex are distinguishable in these families. These are hereafter termed the *Nannaethiops*, *Citharinus*, *Xenocharax* and *Nannocharax* types of pars sustentaculum.

Nannaethiops possesses the simplest form of modification to the pars sustentaculum and os suspensorium in the families Citharinidae and Distichodontidae. In the *Nannaethiops* type pars sustentaculum (Fig. 30) the second and third vertebrae bear paired, ventrally-directed projections arising from their ventrolateral borders, contrary to the plesiomorphous, ventrally unelaborated state of these bones. Furthermore, the os suspensorium in *Nannaethiops* is enlarged and extends anteriorly to contact the posterior margin of the ventral process of the third vertebra. The ventral projections of the second and third vertebrae, together with this anterior process of the os suspensorium, form a longitudinally orientated vertical wall lateral to the dorsal aorta. This structure also serves as a broad area of attachment for the connective tissue sheath associated with the dorsal aorta and coeliac artery. Such adaptations, either in the *Nannaethiops* form or further derived states, are common to all species of the families Citharinidae and Distichodontidae. On the basis of their unique nature within characoids these modifications are hypothesized as being synapomorphous for these families.

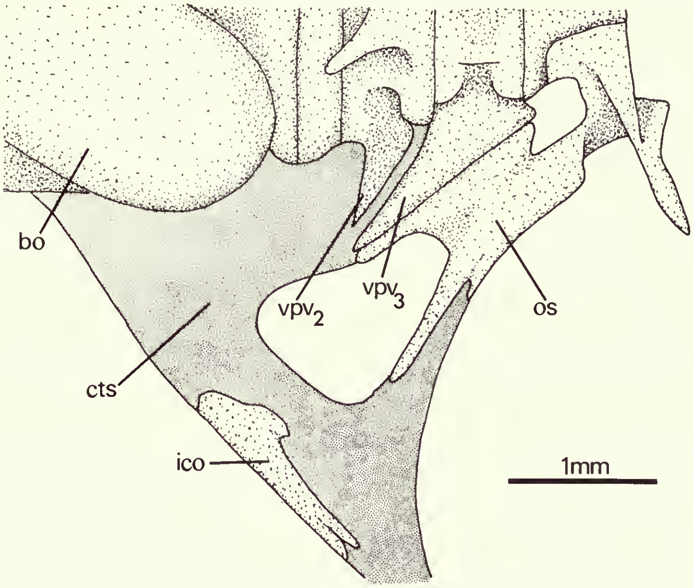

Fig. 31 *Citharinus citharus*, juvenile, posteroventral section of neurocranium, ventral portion of pars sustentaculum, connective tissue sheath and independent coeliac ossifications, left lateral view, Weberian ossicles removed.

As noted previously, the *Nannaethiops* type of pars sustentaculum and os suspensorium is the ontogenetic precursor of more complex structures in citharinids and some other distichodontids. One of the more elaborate alterations of this system is common to *Citharinus* and *Citharidium*. In the smallest individuals of *Citharinus* examined, the pars sustentaculum is similar to the *Nannaethiops* type other than for the slightly more anteroventrally expanded os suspensorium and a pair of slight ossifications along the anterior surface of the coeliac sheath. Later in ontogeny, juveniles of *Citharinus* and *Citharidium* possess the pars sustentaculum and os suspensorium form illustrated in Fig. 31. The ventral processes of the second and third vertebrae are more anteroventrally produced than in the *Nannaethiops* pattern or earlier in ontogeny. Similarly, the os suspensorium is anteroventrally expanded into a prominent, ventrally-directed process that partially encompasses the connective tissue band on the anteromedial surface of the swimbladder. The os suspensorium is also expanded anterodorsally to surround the lateral surface of the dorsal aorta and tightly contact the rear of the expanded ventral process of the third vertebrae

Finally, the coeliac sheath is encompassed anteroventrally by a prominent ossification derived from the independent ossifications present earlier in ontogeny.

With increasing age the os suspensorium, the ventral process of the second and third vertebrae and the independent ossifications of the coeliac sheath coalesce with each other and with the posterior projections of the parasphenoid and ventral projections of the basioccipital. In large individuals of *Citharinus* and *Citharidium* this results in a triangular, highly ossified structure which corresponds in shape to, and largely replaces, the connective tissue sheath present earlier in ontogeny (Fig. 32). This complex is anteriorly continuous with the elongate posterior ramus of the parasphenoid and encompasses the dorsal aorta laterally, ventral to the first three vertebrae.

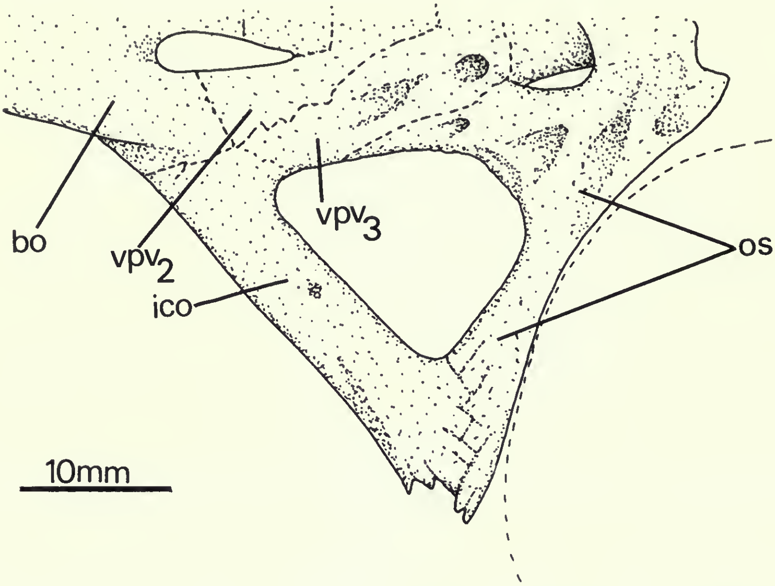

Fig. 32 *Citharinus citharus*, adult, posteroventral section of neurocranium and ventral portion of pars sustentaculum complex, left lateral view, Weberian ossicles removed. The dotted line indicates the position of the anterior chamber of the swimbladder.

Similarly, the coeliac artery is surrounded laterally and ventrally from its divergence from the dorsal aorta to its point of contact with the peritoneal covering of the anterior chamber of the swimbladder. Posteriorly the third portion of this structure consists of a thick bony strut formed by a ventral projection of the os suspensorium. This portion of the complex serves as an expanded area of attachment for the peritoneal layer covering the anterior swimbladder chamber. These modifications of the pars sustentaculum and os suspensorium, together with the strong attachment of the neural process of the Weberian apparatus to the supraoccipital, eliminate any possibility of motion, either between the vertebrae forming the pars sustentaculum or between the pars sustentaculum and the skull. With increasing age, these ossifications expand further so that in the largest citharinid examined (a skull of *Citharinus citharus*, 170 mm from snout to rear of the fourth vertebrae) the processes surrounding the dorsal aorta and coeliac arterly are nearly in contact with their fellows along the internal midline of the complex.

Examination of the Weberian apparatus in characoid outgroups has failed to reveal modifications homologous to those of citharinids, nor have such adaptations been encountered among other ostariophysans. An analogous envelopment of the dorsal aorta and coeliac sheath has been found in the Neotropical characoid genera *Anostomus*, *Leporinus*, *Schizodon* and *Laemolyta*. In these genera the parasphenoid bears posteriorly-directed processes which laterally encompass the dorsal aorta ventral to the basioccipital and first vertebra. In large individuals of these genera, these parasphenoid processes extend posteroventrally along the lateral surface of the strongly developed coeliac sheath, and an independent ossification overlies the dorsal aorta laterally under the first three vertebrae. Although similar in superficial form to those of citharinids, these ossifications in anostomids differ in their ontogenetic origins and are thus considered non-homologous with those of citharinids although synapomorphous for some or all anostomids.

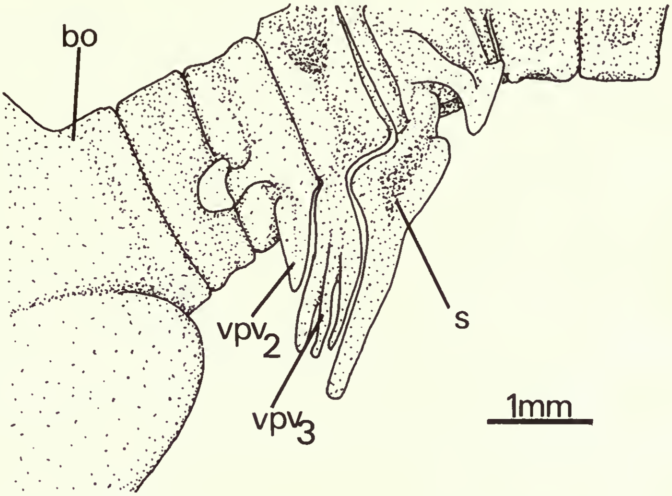

Fig. 33 *Xenocharax spilurus*, posteroventral section of neurocranium and ventral portion of pars sustentaculum, left lateral view, Weberian ossicles removed.

The second apomorphous modification of the *Nannaethiops* type of pars sustentaculum and os suspensorium occurs in the monotypic distichodontid genus *Xenocharax*. In this species the longitudinal axis of the first four vertebrae is strongly angled posterodorsally with respect to the skull and anteroventrally relative to the longitudinal axis through the remaining abdominal vertebrae (Fig. 33). The shift in the axis of these vertebrae is reflected in two adaptations. Firstly, the axis through the chain of the Weberian ossicles is nearly horizontal in *Xenocharax*, rather than demonstrating the posteroventral slope generalized for characoids. This shift is, however, a consequence of the reorientation of the anterior vertebrae with respect to the skull, rather than a repositioning of the ossicles relative to the pars sustentaculum. The second adaptation of the *Xenocharax* os suspensorium is consequent upon the retention by this genus of the primitive relationship of the os suspensorium and the anterior chamber of the swimbladder. Due to the reorientation of the pars sustentaculum with respect to the vertebral column, this alignment represents a marked decrease in the angle between the axis of the os suspensorium and that of the longitudinal axis of the vertebrae of the pars sustentaculum. This alteration is of sufficient magnitude so that the ventral tip of the os suspensorium extends to below the first or second vertebrae. This contrasts to the generalized characoid condition where it reaches only to below the third vertebra.

The fourth and final form of pars sustentaculum among citharinids and distichodontids occurs in some *Nannocharax* species. The species of this genus range from moderately deep-bodied, generalized forms such as *N. multifasciatus*, *N. ansorgei* and *N. minutus* to ventrally-flattened, bottom-dwelling species such as *N. brevis*, *N. gobioides*, *N. niloticus* and *N. intermedius*. One of the myriad adaptions to a bottom-dwelling habit demonstrated by the latter group of species is a restructuring of the pars sustentaculum and the first and second pleural ribs. Generalized *Nannocharax* species have the basically *Nannaethiops* type of pars sustentaculum. In the specialized forms, however, the proximal section of the first pleural rib is expanded anteriorly to form a prominent flange extending over the dorsal surface of the anterior swimbladder chamber. The second pleural rib has a similar, though posteriorly-directed and somewhat smaller, process proximally. Further distally this rib also bears an anteriorly directed flange extending along the lateral wall of the anterior chamber of the swimbladder. More notably, the ventral processes of the second vertebra are expanded into a common, transverse, plate-like structure covering the anterior and anteroventral surfaces of the anterior chamber of the swimbladder (Fig. 34). Associated with these expanded ventral processes of the second vertebra is the development of a bony tube along the anteromedial face of this plate. This canal surrounds the coeliac artery from its point of origin to the point where, plesiomorphously, it contacts the anterior chamber of the swimbladder. It should be emphasized that although superficially similar to the bony tube around the coeliac artery in citharinids, this channel in *Nannocharax* is formed by a process of the second vertebra rather than by the citharinid independent ossifications.

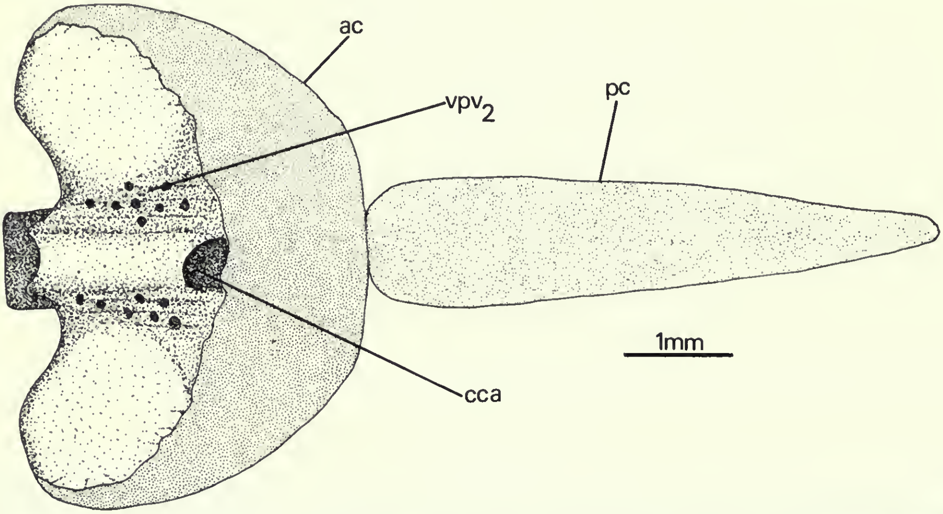

Fig. 34 *Nannocharax niloticus*, swimbladder and bony capsule of anterior swimbladder chamber, ventral view.

Such an encapsulation of the anterior swimbladder chamber has not been reported previously among characoids or encountered elsewhere in the superfamily during this study and undoubtedly represents a synapomorphy for some *Nannocharax* species. Functionally, this partial encapsulation of the swimbladder appears to be related to the bottom-dwelling habits of the species possessing it, as is the case in cobitids, various catfish groups and perhaps the small capsules around the anterior swimbladder chamber in some gymnotids (e.g. *Rhamphichthys rostratus*).

Derived states of the Weberian apparatus in the families Citharinidae and Distichodontidae are:

1. the expanded os suspensorium and the ventrolateral projections of the second and third vertebrae common to all citharinids and distichodontids at some point in ontogeny.
2. the highly ossified triangular pars sustentaculum complex of citharinids.
3. the marked reduction in the angle between the axis of the os suspensorium and that of the pars sustentaculum in *Xenocharax*.
4. the expansion of the ventral processes of the second vertebra and modifications of the first and second pleural rib to partially encapsulate the anterior chamber of the swimbladder in some *Nannocharax* species.

Postcleithra

The pectoral girdle of citharinids and distichodontids is distinctive in having a maximum of two postcleithra rather than the three postcleithral elements that characterize most characoids. The upper postcleithrum in these families overlaps the junction between the cleithrum and supracleithrum and is homologous with the element termed postcleithrum 1 in *Byrcon meeki* by

Weitzman (1962). The remaining postcleithrum in citharinids and distichodontids is located posteromedial to the cleithrum and has the form of an elongate plate with a pronounced anteroventral strut that is ventrally continuous with a rod-like process (Fig. 35a) (see also below with respect to *Phago* and *Belonophago*). In overall form this postcleithral element is very similar to the flat, ovoid postcleithrum 2 and the separate rod-like postcleithrum 3 overlapping and ventral to the former that occupy this region in most characoids. Because of this similarity in form, the ventral postcleithral element of citharinids and distichodontids is hypothesized to represent an apomorphous, fused postcleithrum 2 and 3. *Nannocharax* and *Hemigrammocharax*, in addition, lack the dorsal postcleithral element (postcleithrum 1) that plesiomorphously overlies the junction between the cleithrum and supracleithrum. A final postcleithral character of note in these families is the expansion of the ventral postcleithral element in *Phago* and *Belonophago* to form a rigid strut around the posterior border of the pectoral fin base (Fig. 35b).

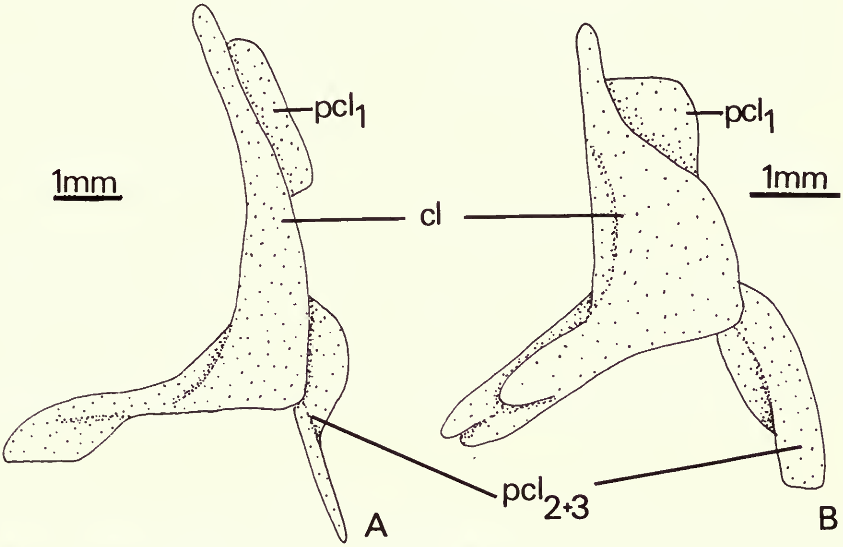

Fig. 35 Cleithrum and postcleithra of A. *Citharidium ansorgei*, B. *Phago intermedius*.

Pelvic bone

The form of the pelvic bone shows considerable variation from the generalized characoid condition both throughout and within the assemblage that constitutes the families Citharinidae and Distichodontidae. The pelvic bone of anotophysans and generalized characoids has anteriorly a single tapering process braced by a longitudinal ridge. However, among citharinids and particularly distichodontids, the pelvic bone has two anterior processes giving it an anteriorly bifurcate form (Fig. 36a). The longer lateral process extends almost directly anteriorly and bears a longitudinal ridge along its dorsal surface. The smaller medially slanting process, in turn, has a shorter ventral ridge. A somewhat bifurcate pelvic bone also occurs in various neotropical characoid groups, but in none of them is the bifurcation as pronounced as that in citharinids and distichodontids.

Further modifications to the pelvic bone occur in bottom-dwelling *Nannocharax* species (*N. niloticus*, *N. gobioides*, *N. intermedius* and *N. fasciatus*) in which the pelvic bone is distinctly widened anteriorly to form a broad plate-like structure (Fig. 36b). This modification, the congruent expansion of the ischiac process of the pelvic bone and the elongation of the pelvic fin rays is evidently an adaptation to the bottom-dwelling habits of these species.

Caudal skeleton

The caudal skeleton of citharinids and distichodontids exhibit several characters of interest both

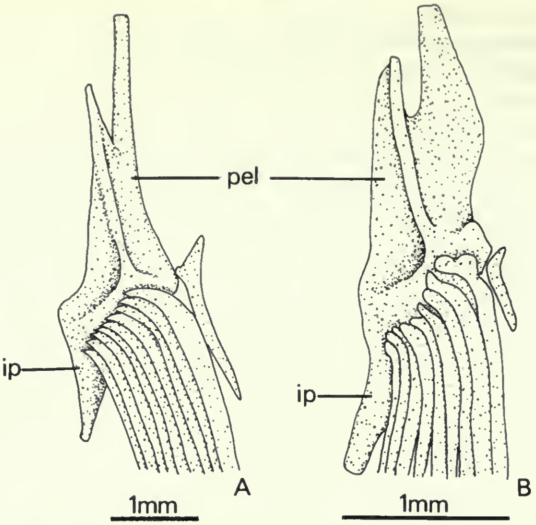

Fig. 36 Pelvic girdle of A. *Xenocharax spilurus*, B. *Nannocharax niloticus*.

relative to the question of the monophyletic nature of the complex formed by these families and to the hypothesis of relationships within the assemblage. The hypural fan form hypothesized plesiomorphous for characoids consists of six separate hypural elements. All citharinids and distichodontids differ from this condition in having hypurals 1 and 2 (the ventral elements) fused into a single unit not articulating with the fused PU_1 and U_1 (Fig. 37).

Such an apomorphic fusion of the two ventral hypurals also occurs within the Characoidea in the South American family Hemiodontidae (including *Anodus*), the characid subfamily Serrasalminae and the African characid *Lepidarchus adonis* (Roberts, 1966). As noted earlier the

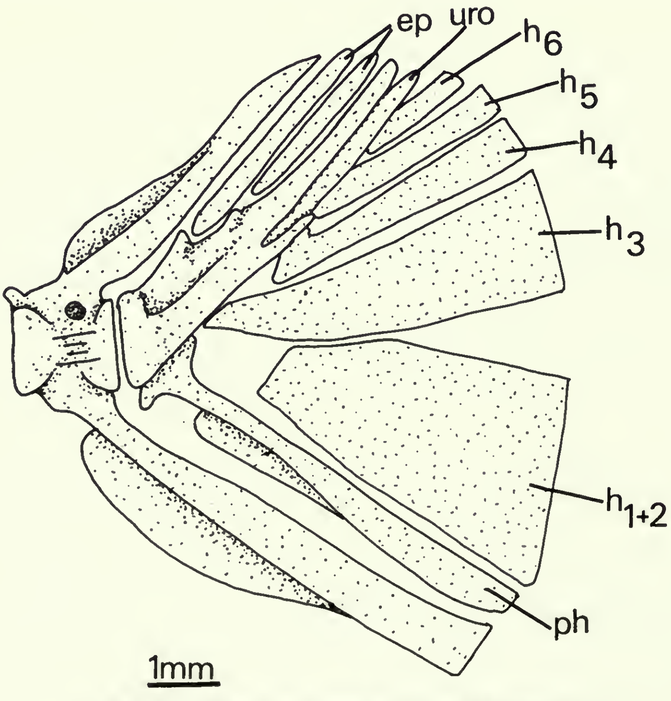

Fig. 37 *Xenocharax spilurus*, caudal skeleton.

members of the Hemiodontidae possess a rhinosphenoid; an apomorphous median ossification unique to various Neotropical characoids. With the exception of hemiodontids, all members of these rhinosphenoid-bearing groups examined during this study have separate hypurals. Similarly, although the exact relationships of the Serrasalminae are unknown, their multicuspidate dentition ties them to various Neotropical groups which lack any hypural fusions. Finally, *Lepidarchus* is a member of the African Characidae (Roberts, 1966) whose members are otherwise characterized by six separate hypurals.

Two other South American characoid groups have fused hypurals 1 and 2. However, in each of these cases the fused hypural plate differs from that of citharinids and distichodontids in such a way as to cast doubt on the homology of this fusion with that in the latter families. In the Cynodontini the genera *Hydrolycus* and *Cynodon* have hypurals 1, 2 and 3 joined into a large plate encompassing the ventral and part of the dorsal portions of the hypural fan. However, the cynodontine genus *Rhaphiodon*, has hypurals 2 and 3 fused, but separate from hypural 1. Finally, *Roestes*, the most plesiomorphous cynodontine (Howes, 1976), has a completely separate hypural fan. Thus it is most parsimonious to assume that the phylogenetic progression of hypural fusion of cynodontines is a joining of hypurals 2 and 3 followed by the fusion of the resultant plate with hypural 1. Such a sequence does not demonstrate a fusion homologous with the fused hypurals 1 and 2 that characterize citharinids and distichodontids. Finally, fused hypurals 1 and 2 have also been discovered in *Crenuchus* and *Poecilocharax*. The fused hypurals in these genera differ, however, from the pattern in citharinids and distichodontids in being joined to the fused PU_1 and U_1.

The number of separate hypural elements is further reduced in *Neolebias*, *Nannaethiops* and *Paradistichodus* in which only three upper hypurals exist. Although the question of whether this reduction is a consequence of the fusion of hypurals 5 and 6, or a loss of the latter, has not been resolved, such a reduction is nonetheless considered to be a derived feature. Finally, a reduction from the two epurals plesiomorphous for citharinids and distichodontids has occurred in *Paradistichodus*, *Phago* and *Belonophago* in which only one epural is present.

Scale form

Unlike most anatomical features, the scale form among members of the Characoidea exhibits little variation at the gross morphological level. The majority of characoids are characterized by the possession of a simple cycloid scale form. Within the families Citharinidae and Distichodontidae, however, this seemingly plesiomorphous scale form is limited to the genus *Citharinus*. *Citharidium* has ctenoid scales, while all distichodontids have a second, non-homologous form of serrate scales.

In *Citharidium* the prominent, distinctly pointed ctenii are continuous with the main body of the scale (Fig. 38a). In this scale form a strong ridge extends from the scale body radially along the centre of each cteni, with the distal circuli diverging outwards along the ridge. The members of the family Distichodontidae, in contrast, possess a very different type of ctenoid scale, the simplest form of which is illustrated in Fig. 38b. In the distichodontid ctenoid scale, the scale body is comparable to that of a typical characoid scale except for a shift of the scale focus towards the scale margin. Along the scale margin there occurs a line of irregular ctenii that vary in number between different taxa. These ctenii differ from those of *Citharidium* in being formed by a series of independent ossifications attached to the scale body and each other by unossified connective tissue.

Examination of the ctenoid scales reported in other characoid groups has shown the term to be applied to an assemblage of very different scale types characterized by various forms of serrate posterior margins. In *Cynopotamus* and other genera in the Neotropical tribe Characini the ctenoid nature of the scales is a consequence of a series of spicules along the posterior margin and exposed lateral surface of the scale. The ctenoid scales of the tetragonopterine *Ctenobrycon*, various curimatids and the prochilodontid genus *Prochilodus* are characterized by an irregularly notched posterior scale margin, whereas the curimatid genus *Psectrogaster* has definite although somewhat irregular ctenii. However, none of the above forms of ctenoid scales is comparable

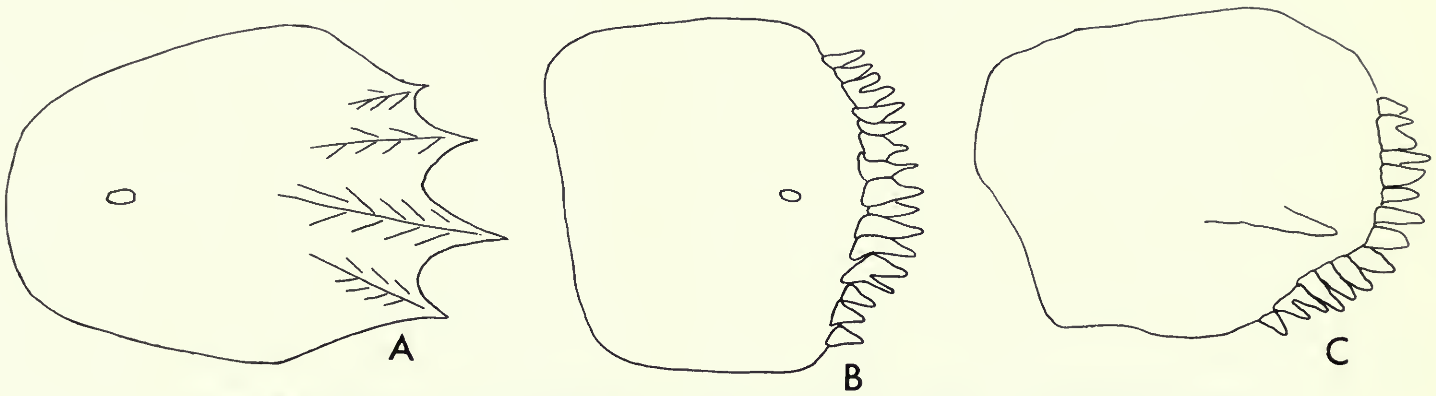

Fig. 38 Scale form of A. *Citharidium ansorgei*, B. *Xenocharax spilurus*, C. *Belonophago tinanti*.

to those in the African families under discussion. In the South American genus *Ctenolucius* the scales bear strong ctenii formed primarily by posterior continuations of the pronounced ridges that radiate outwards from the focus. In the closely related *Boulengerella* a less well-developed form of the same scale type occurs. Although these scale types approximate to that in *Citharidium*, they differ in the form of the ridges and in possessing strong radii which are totally lacking in that genus. These differences and the large number of derived characters uniting *Citharidium* into a monophyletic unit with *Citharinus* (which retains the plesiomorphous cycloid scale form) support the hypothesis that the *Ctenolucius* and citharinid forms of ctenoid scales were acquired independently.

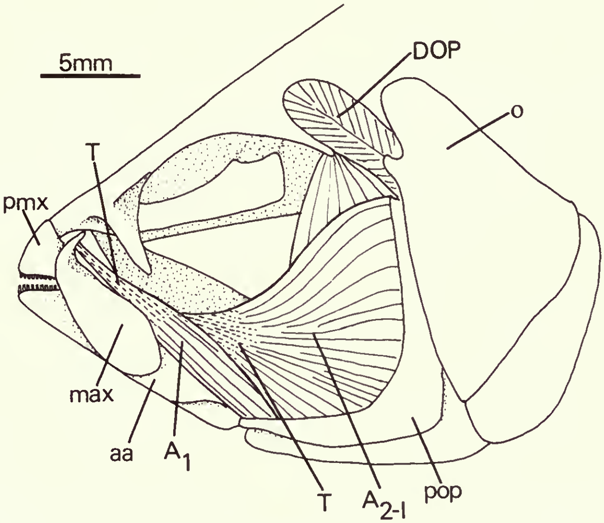

Fig. 39 *Xenocharax spilurus*, superficial cranial musculature, lateral view.

Although the distichodontid form of ctenoid scale does not appear to be approximated within characoids, a similar ctenoid scale with serrations formed by a series of independent ossifications occurs in the anatopysan ostariophysan *Gonorhynchus greyi*. However, the similarity in scale form between such phylogenetically separated members of the Ostariophysi undoubtedly represents independent acquisitions.

The distichodontid form of ctenoid scale undergoes further modifications in the genera *Phago* and *Belonophago*. In these taxa the greatly thickened scales and strong connective tissue bands joining them result in a bony but flexible body covering. Furthermore, as a consequence of their elongate cylindriform bodies, the relatively large scales in these genera are distinctly flexed horizontally. This flexure is especially pronounced in the vertically elongate scales of *Phago*. *Phago* and *Belonophago* have a distinct ossified bump overlying the scale focus, with this structure produced into a posteriorly directed spinous process in *Belonophago* (Fig. 38c).

The final character of note in the scalation of these families is the form and extent of development of the lateral line system. Although the plesiomorphous lateral line form among characoids is unknown, it is noteworthy that citharinids and distichodontids have a straight or nearly straight lateral line. This contrasts with the distinctly ventrally-curved lateral line in all other African and most Neotropical characoids. A reduction from a complete lateral line occurs in all *Neolebias* and *Hemigrammocharax* species. However, Roberts (1967) has questioned whether the reduced lateral line of *Hemigrammocharax* represents single or multiple reductions from the complete lateral line of *Nannocharax*. Two species of *Hemistichodus* (*lootensi* and *mesmaekersi*) have a distinctive medially interrupted lateral line.

Myology

The osteological characters described above have included a variety of alterations of the jaws, the jaw suspensorium, the operculum and the parts of the neurocranium associated with these systems. Congruent with these osteological changes are a series of adaptations in the cheek and opercular musculature of these genera.

In the following discussion the musculature of the distichodontid genus *Xenocharax* will first be described in detail. As far as can be determined from outgroup comparisons to generalized characoids, the myological plan of *Xenocharax* is the least derived overall among citharinids and distichodontids. Thus it serves as a useful basis of comparison for the myological variation that occurs in these families. In the case of *Paraphago*, which is known only from two syntypes and which was consequently not examined myologically, it is assumed that the myological characters of the genus are congruent with those of its monophyletic group. The muscles providing information relevant to a reconstruction of the hypothesized phylogeny of citharinids and distichodontids are the *adductor mandibulae*, the *levator arcus palatini* and the *dilatator operculi*.

The *adductor mandibulae* in *Xenocharax* (Fig. 39) is composed of sections A_1, A_2 (divisible into medial and lateral portions), A_3 and A_W. The A_1 portion of the *adductor mandibulae* is a somewhat tubular muscle extending anterodorsally from its origin on the lateral flange of the horizontal process of the quadrate. It is dorsally encompassed by a connective tissue sheath continuous with the strong tendon that runs along the anterior surface of the muscle. This tendon, in turn, inserts onto the maxilla at the point of merger between the anteromedial maxillary process and the broad lateral plate of the bone.

The remainder of the *adductor mandibulae* consists of the two sections of the A_2 portion of the muscle and medial to these an A_3. Posteriorly the two portions of the A_2 arise in common from the lateral face of the hyomandibula and vertical ramus of the preopercle. Along their posterodorsal borders these portions of the muscle contact the ventrolateral face of the dorsally widened *levator arcus palatini*. Ventrally A_2 has an origin from the lateral face of the horizontal portion of the preopercle and the posteroventral process of the quadrate (the medial portion of A_2 does not arise from the latter element). The A_2 divides into two sections parasagittally slightly anterior to the point where the *levator arcus palatini* passes between the A_2 and A_3 portions of the *adductor mandibulae*. The lateral section of A_2 extends forward over the posterodorsal surface of A_1 to insert onto the posterior edge of the dentary, just dorsal to the articulation of that element with the angulo-articular. The medial portion of A_2, in contrast, has its anterodorsal surface invested by a connective tissue band that is continuous with a prominent tendon extending anteriorly from the forward tip of the muscle and joining a comparable tendon from the A_3. This common tendon inserts onto the A_w and the coronomeckelian ossification (Fig. 40). The A_3 section of the *adductor mandibulae* is posteriorly separated from the medial section of A_2 by the ventral portion of the *levator arcus palatini*. The A_3 arises from the anteromedial surface of the hyomandibula and is surrounded anteriorly by a connective tissue sheath that is continuous with the tendon arising from the medial section of A_2. Finally, the A_w (intramandibular) section of the *adductor mandibulae* is a relatively flat muscle filling the meckelian fossa and attaching to the angulo-articular and dentary.

The *levator arcus palatini* of *Xenocharax* is a triangular muscle, laterally exposed along the posterodorsal region of the cheek. From its origin on the posteroventral portion of the sphenotic spine the *levator arcus palatini* extends ventrally between A_3 and the medial section of A_2 to insert on the anteroventral portion of the hyomandibula. The *dilatator operculi* is a pinnate muscle arising from the broad dilatator fossa of the sphenotic and pterotic and inserting onto a raised ridge along the anterodorsal corner of the opercle.

The above pattern of cheek and opercular musculature is common to *Xenocharax*, *Nannaethiops* and *Neolebias*. Citharinids and other distichodontids differ to varying degrees from the *Xenocharax* cheek musculature pattern. This variation in muscle origins, insertions, proportions and interconnections serves to define a series of multigeneric units within these families.

Citharinus and *Citharidium* have an elongate A_1 portion of the *adductor* mandibulae with a more extensive origin on the horizontal process of the quadrate and the ventral arm of the preopercle than in the *Xenocharax* condition (Fig. 41). More significantly, the citharinid A_1 differs from that of *Xenocharax* in attaching directly to the rear of the dentary rather than tendinously to the maxilla. Citharinids have, however, a ligament running from the point of contact of the A_1 with the dentary to the region of the maxilla where the tendon of A_1 inserts in *Xenocharax*. This ligament, the *ligamentum primordiale* of previous authors, may be homologous to the tendinous band along the anterior surface of the A_1 section of the *adductor mandibulae* in *Xenocharax*. On the basis of outgroup comparisons, the citharinid insertion of the A_1 to the dentary in conjunction with the retention of a distinct *ligamentum primordiale* is hypothesized to be the plesiomorphous characoid condition. The derived attachment of the A_1 to the maxilla in *Xenocharax* together with the seeming incorporation of the *ligamentum primordiale* into its tendon is evidently correlated with the increased upper jaw mobility of distichodontids.

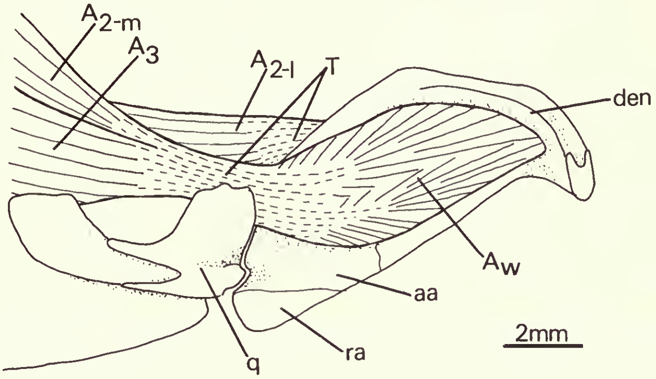

Fig. 40 *Xenocharax spilurus*, *adductor mandibulae*, anterior portions, medial view.

The A_2 portion of the *adductor mandibulae* in *Citharinus* and *Citharidium* arises posteriorly from the lateral surfaces of the hyomandibula and preopercle, but does not extend as dorsal on these elements as in *Xenocharax*. Anteriorly the lateral portion of the A_2 in citharinids inserts onto the rear of the A_w through a tendon that is anteriorly continuous with that of the medial section of A_2. This common insertion contrasts with the separate attachment of these muscles on the dentary and A_W respectively in *Xenocharax*. That portion of the *adductor mandibulae* of citharinids comparable to the A_3 of *Xenocharax* (that portion of the muscle medial to the *levator arcus palatini*) is greatly reduced and usually has the form of a series of muscle slips arising from the hyomandibula and metapterygoid. Furthermore, rather than having a distinct tendon, anteriorly continuous with the anterior tendon of A_2, the slips of muscles forming the A_3 of citharinids attach individually along the inner surface of the medial portion of A_2.

The A_w section of the *adductor mandibulae* in *Citharinus* and *Citharidium* is greatly expanded to fill entirely the large meckelian fossa and extends dorsally over the upper edge of the dentary. The *levator arcus palatini* of these genera, although relatively longer than in *Xenocharax*, has a similar origin and insertion apart from an expanded insertion posterodorsally on the preopercle. The *dilatator operculi* is significantly larger than that of *Xenocharax* and totally fills the large dilatator fossa on the sphenotic, pterotic and lateral edge of the frontal. This pinnate muscle inserts on the distinctive, elongate opercular spine that extends anterodorsally towards the middle of the fossa in citharinids.

Within distichodontids, several genera and generic assemblages show various modifications of the *Xenocharax* pattern of cheek musculature. In *Paradistichodus* the overall proportions of the muscles are changed, perhaps as a consequence of the elongate head that characterizes the genus. The A_1 portion of the *adductor mandibulae* is notably elongate and the muscle extends along the tendon anterodorsally, nearly to the maxilla. Overall, the A_2 is smaller than in *Xenocharax* and arises solely from the ventral half of the preopercle and hyomandibula. This reduction of the A_2 is especially notable in the longitudinal extent of the lateral section of the muscle which consequently attaches to the dentary through an elongate tendon.

Distichodus, *Nannocharax* and *Hemigrammocharax* have a series of modifications of the *adductor mandibulae* correlated with their unique jaw morphology (Fig. 42). The elongate A_1

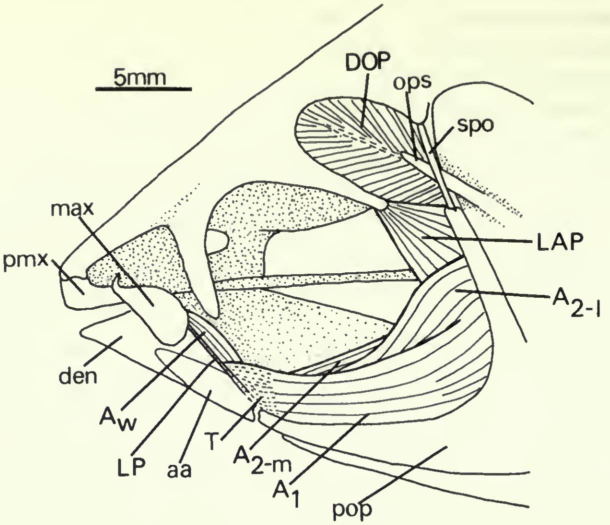

Fig. 41 *Citharinus citharus*, superficial cranial musculature, lateral view.

portion of this muscle arises from the quadrate and extends anteriorly to attach to the maxilla by way of a ligament running across the lateral face of the dorsally expanded dentary. As in *Xenocharax* the A_2 section of the *adductor mandibulae* is subdivided into medial and lateral segments with a prominent A_3 also present. However, as a consequence of the radically restructured jaw form of these genera, the relationships between the sections of the *adductor mandibulae* are somewhat altered. In other distichodontids the anterior sections of A_2 and A_3 run in parallel and the lateral portion of A_2 inserts lateral to, or only slightly dorsolateral to, the point where the joined tendon of A_3 and the medial portion of A_2 contacts the A_W. In *Distichodus*, *Nannocharax* and *Hemigrammocharax*, in contrast, the insertion of the lateral portion of A_2 is distinctly dorsal to the level where the combined tendon from A_3 and the medial section of A_2 attach onto the coronomeckelian ossification. The A_W of *Distichodus*, *Nannocharax* and *Hemigrammocharax* arises from the dorsal edge of the latter tendon and extends from distinctly posterior of the rear of the angulo-articular forward onto the bone. Both the origin of the A_W solely from the dorsal border of the ligament and its posterior position relative to the angulo-articular appear apomorphous relative to the generalized characoid condition. An additional

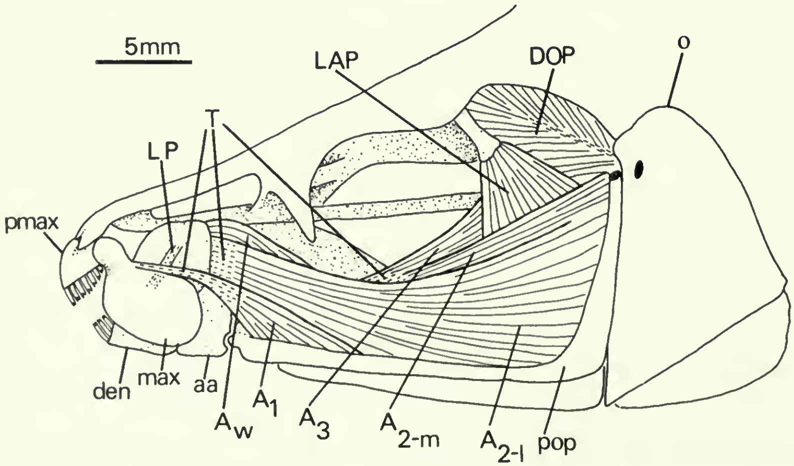

Fig. 42 *Distichodus lusosso*, superficial cranial musculature, lateral view. Dashed line on maxilla indicates attachment of *ligamentum primordiale*.

consequence of these osteological and myological alterations is a shift of the relative position of the *ligamentum primordiale* and the tendon of A_1. Instead of running in common or parallel as in the plesiomorphous condition, the connective tissue bands in these genera cross at right angles, with the tendon of A_1 passing over the *ligamentum primordiale*.

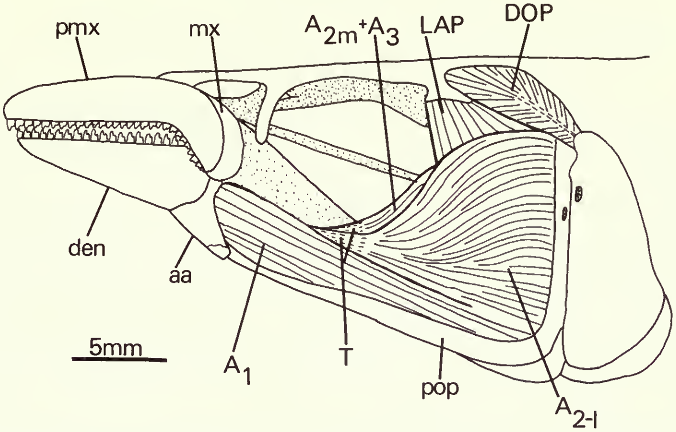

Fig. 43 *Ichthyborus quadrilineatus*, superficial cranial musculature, lateral view.

As discussed earlier the ventral edge of the sphenotic spine undergoes a progressive phylogenetic enlargement within the unit formed by *Distichodus*, *Hemigrammocharax* and *Nannocharax*. Congruent with this alteration of the spine is an expansion in the extent of the origin of the *levator arcus palatini*. This trend is especially pronounced in *Nannocharax* and *Hemigrammocharax* in which the broad ventrally concave sphenotic process serves as an expanded area of origin for the *levator arcus palatini*. Furthermore, in these genera the *dilatator operculi* rather than having the hypothesized plesiomorphous origin from the dilatator fossa has a broad attachment to the lateral surface of the sphenotic. This shift from the generalized characoid condition is carried further in some of the larger *Nannocharax* species examined (*N. fasciatus* and *N. elongatus*).

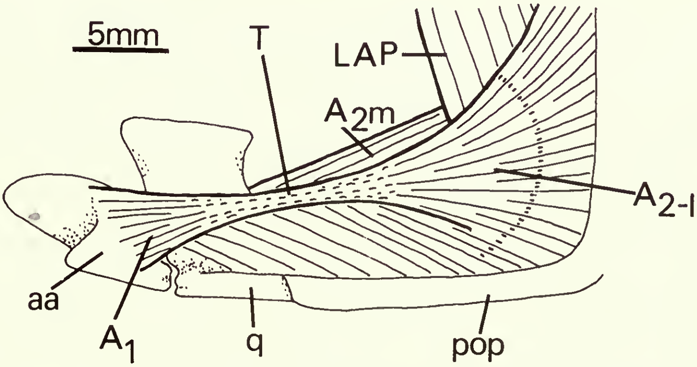

Fig. 44 *Ichthyborus besse*, *adductor mandibulae*, lateral view.

In these species the anterior portion of the *dilatator operculi* arises from the anterior face of the sphenotic and passes medial to the *levator arcus palatini* to insert on the anterodorsal process of the opercle. The broad, shallow depression on the sphenotic and pterotic of *Nannocharax* and *Hemigrammocharax* does not serve as a dilatator fossa, but is instead occupied by the plate-like dermosphenotic present in these genera.

The remaining distichodontid genera, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, have the A_1 portion of the *adductor mandibulae* arising from the trough formed by the lateral processes of the quadrate and preopercle. This muscle inserts on the posterolateral and posterior surface of the angulo-articular (Figs 43, 44). Such an insertion differs radically from the tendinous attachment of this muscle section to the maxilla in all other distichodontids. This change and the congruent loss of a definitive *ligamentum primordiale* appears consequent upon the radically altered upper jaw morphology of these genera. These changes result in the elimination of the functional advantage that an attachment of the A_1 to the maxilla provides in less derived forms of distichodontid jaws. These genera, with the exception of *Hemistichodus*, also have a significantly enlarged origin of the *adductor mandibulae* on the lateral and medial surfaces of the hyomandibula and the lateroventral portions of the sphenotic and pterotic. This expanded origin is particularly pronounced in *Eugnatichthys*.

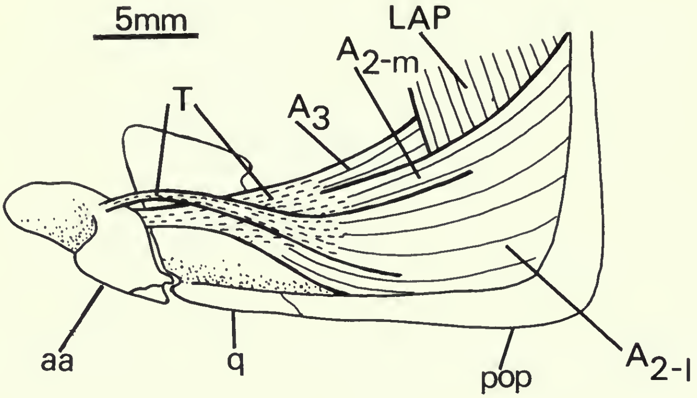

Fig. 45 *Ichthyborus ornatus*, *adductor mandibulae*, lateral view, A_1 portion removed.

Within the above assemblage, both *Ichthyborus* and *Eugnatichthys* present further apomorphic myological characters. The A_1 of *Ichthyborus besse* is distinctive in having its lateral portion autapomorphously altered into a distinct triangular muscle slip which attaches to the lateral portion of A_2 *via* a connective tissue band (Fig. 44). In addition, all *Ichthyborus* species are distinctive among distichodontids in having the lateral portion of the A_2 inserting on the angulo-articular, contrary to the plesiomorphous attachment of this muscle segment on the dentary. This insertion is through an elongate anterior tendon in *Ichthyborus ornatus*, *I. monodi* and *I. quadrilineatus* (Fig. 45) and by way of the aforementioned modified section of the A_1 in *I. besse* (Fig. 44).

Eugnatichthys has the primitively single A_3 portion of the *adductor mandibulae* parasagittally subdivided into two sections. The lateral portion of the A_3 in this genus extends anteriorly to join the medial section of A_2 and inserts in common with that muscle directly on the dentary. This insertion contrasts with the plesiomorphous insertion of the A_3 on the coronomeckelian ossification, an insertion that is retained by the medial portion of the A_3 section of the adductor mandibulae of *Eugnatichthys*.

The *levator arcus palatini* in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* has an apomorphous expanded origin on the ventral (primitively anterior) surface of the posteroventrally sloping or horizontal sphenotic spine characteristic of these genera. *Phago* and *Belonophago*, in turn, have the muscle origin further expanded onto the ventral face of the frontal in the posterodorsal orbital region; an adaptation unique to these genera among characoids examined. Finally, the *levator arcus palatini* of

Eugnatichthys, *Phago* and *Belonophago* has a distinctly reduced vertical extent relative to that of other distichodontids and consequently does not directly insert onto the hyomandibula. Instead, these genera have the muscle inserting onto that element *via* a broad aponeuroses.

In summary, hypothesized derived states of the *adductor mandibulae*, *levator arcus palatini* and *dilatator operculi* among citharinids and distichodontids are:

1 the insertion of the A_1 portion of the *adductor mandibulae* on the maxilla in *Xenocharax*, *Neolebias*, *Nannaethiops*, *Paradistichodus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax*. This attachment is hypothesized, however, to have been secondarily lost in all other distichodontids.

2 the insertion of the lateral section of the A_2 portion of the *adductor mandibulae* to the A_W *via* a tendon in citharinids.

3 the reduction of the A_3 portion of the *adductor mandibulae* in citharinids.

4 the greatly expanded A_W portion of the *adductor mandibulae* in citharinids.

5 the expanded *dilatator operculi* in citharinids.

6 the reduced lateral portion of the A_2 section of the *adductor mandibulae* in *Paradistichodus*.

7 the elongation of the A_1 portion of the *adductor mandibulae* in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

8 the relatively dorsal insertion of the lateral portion of A_2 in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

9 the posterior origin and expanded extent of the A_W portion of the *adductor mandibulae* in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

10 the expanded origin of the *levator arcus palatini* on the ventrally broadened sphenotic spine in *Nannocharax*, *Hemigrammocharax* and some *Distichodus* species.

11 the shift of the origin of the *dilatator operculi* to the lateral surface of the sphenotic in *Nannocharax* and *Hemigrammocharax*.

12 the insertion of the lateral portion of the A_2 on the angulo-articular in *Ichthyborus*.

13 the expansion of the origin of the A_2 section of the *adductor mandibulae* onto the medial surface of the hyomandibula and ventral surfaces of the pterotic and sphenotic in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera also have the origin of the *levator arcus palatini* expanded onto the anterior surface of the sphenotic spine.

14 the partial origin of the *levator arcus palatini* from the ventral surface of the frontal in *Phago* and *Belonophago*.

15 the reduction of the vertical extent of the *levator arcus palatini* and its insertion on the hyomandibula through an aponeuroses in *Eugnatichthys*, *Phago* and *Belonophago*.

Swimbladder, intestinal and epibranchial organ forms

Swimbladder

Within the assemblage consisting of the Citharinidae and Distichodontidae, the form of both the anterior and posterior chambers of the swimbladder undergoes several modifications. The generalized swimbladder morphology in characoids consists of two chambers connected by a short narrow tube. The rotund anterior chamber is slightly elongate and is attached by the peritoneal layer surrounding it to the os suspensorium and the triangular connective tissue complex associated with the pars sustentaculum of the Weberian apparatus. The posterior chamber is of slightly greater diameter than the anterior and several times the longitudinal extent.

Although the plesiomorphous relative proportions of the chambers of the swimbladder among characoids is presently unknown, it is noteworthy that in both citharinids and distichodontids the posterior chamber of the swimbladder is distinctly elongate with respect to the anterior (approximately four times the longitudinal length). Despite this uncertainty about the phylogenetic polarity of an elongate posterior swimbladder chamber, the possession of such a structure is, nonetheless, at least congruent with the hypothesis of the monophyly of the unit formed by citharinids and distichodontids among characoids. Is should be emphasized, however, that even if apomorphous for characoids, such an elongate posterior chamber of the swimbladder is also characteristic of the South American characoid family Hemiodontidae and occurs in various forms in some Neotropical characids (e.g. Iguanodectinae, see Vari, 1977).

Within the Distichodontidae, the evenly curved oblong anterior and elongate posterior swimbladder chambers that are plesiomorphous for the family are modified in *Hemigrammocharax* and *Nannocharax*. These genera have anteriorly-directed diverticulae of the anterior swimbladder chamber. These diverticulae extend from the anterior face of the chamber lateral to the ventral process of the os suspensorium and the posterior portion of the triangular connective tissue complex associated with the pars sustentaculum. The extent of these diverticulae range from the slight bulges of *Hemigrammocharax* and generalized *Nannocharax* species to the pronounced anterior diverticulae found in specialized *Nannocharax* species such as *N. niloticus*, *N. gobioides* and *N. intermedius*. The latter *Nannocharax* species also have the posterior swimbladder chamber greatly reduced to a small tubular structure (Fig. 34); an adaptation evidently correlated with their bottom-dwelling habits.

Intestinal form

Two modifications of the morphology and convolution patterns of the intestinal tract distinguish citharinids within the complex formed by the families Citharinidae and Distichodontidae. On the basis of information from ontogenetic and outgroup comparisons, the plesiomorphous form of the intestinal tract among characoids appears to be a moderately looping, smooth-walled system. In both *Citharinus* and *Citharidium*, however, the intestine is elaborated into a highly convoluted system (see Daget, 1962, Fig. 9) characterized by distinctive multiple outpocketings of its terminal loop. Whereas the elongation of the intestine is evidently correlated with the microphagous habits of these genera, the functional significance of the intestinal outpocketings is obscure.

Epibranchial organ form

Epibranchial organs of differing levels of complexity have been described for a variety of Neotropical and African characoids (see Nelson, 1967, p. 73). Within the families under discussion, a slightly developed diverticula in the posterior portion of the gill arches has been reported among distichodontids in *Paradistichodus* (Daget, 1958, p. 1368), *Distichodus* (Daget, 1959, p. 1289), *Xenocharax* (Daget, 1960, p. 41), *Nannocharax* (Daget, 1961, p. 172) and *Neolebias* (Daget, 1965, p. 9). The structure has also been found in *Nannaethiops* and *Hemigrammocharax* during this study. Daget reported that the epibranchial organ was absent in *Ichthyborus besse* (1967, p. 145) and *Hemistichodus* (1968, p. 16). This study has also found such outpocketings to be lacking in the remaining *Ichthyborus* species, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Phago* and *Belonophago*. The lack of epibranchial organs in these genera is considered to be an apomorphous secondary loss on the basis of the presence of such outpocketings in the Citharinidae, which is the sister group to distichodontids, and in all other distichodontids.

Citharinus and *Citharidium*, in contrast, have greatly elaborated epibranchial organs. In these genera the diverticulae are expanded into lobulate muscular structures (Fig. 46) with ramifying internal chambers supported by spicules of bone (see Daget, 1962*a*, Figs 7, 8). Prominent epibranchial organs also occur in the Neotropical characoid families Prochilodontidae and Curimatidae. In neither of those families, however, are these outpocketings as greatly developed as they are in citharinids. Neither do the epibranchial organs of the Neotropical groups have the distinctive lobed forms of those in the Citharinidae. Thus the form of the citharinid epibranchial organs is considered synapomorphous for *Citharinus* and *Citharidium* among characoids.

Olfactory bulbs

Among anotophysans and most characoids the olfactory bulb lies immediately anterior to, and in contact with, the telencephalon and is laterally enclosed by the orbitosphenoid. In this state the olfactory nerve passes anteriorly either through the anteromedial opening in the orbitosphenoid or through foramina in that bone, and extends anterolaterally to the olfactory foramen of the lateral ethmoid. Citharinids and distichodontids, in contrast, have the olfactory bulbs shifted anteriorly to contact or nearly contact the posterior surface of the lateral ethmoid. This shift in olfactory bulb position results in a shortening of the olfactory nerve and an elongation of the olfactory tract. These alterations of the olfactory system are hypothesized apomorphous for these families within characoids. This hypothesis is based both on the widespread distribution of a posterior position of the olfactory bulb among teleosts in general and characoids in particular, and on the ontogenetic anterior movement of the bulb that has been observed in various citharinids and distichodontids.

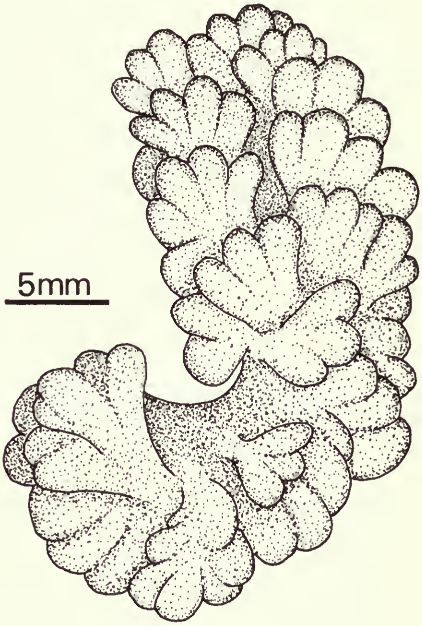

Fig. 46 *Citharidium ansorgei*, epibranchial organ, left lateral view.

Although an anterior position of the olfactory bulb is generalized for cyprinoids and siluroids, among characoids examined during this study such a forward location of the bulb has been found only in citharinids, distichodontids, the genus *Salminus*, some african characids and the family Parodontidae. Adults of *Salminus maxillosus* have the olfactory bulb immediately posterior of the lateral ethmoid, a shift evidently reflected in ontogeny since young *S. hilarii* have the olfactory bulb relatively more posteriorly located. The significance of the forward position of the olfactory bulb for an understanding of the relationships of these enigmatic South American characoids to citharinids and distichodontids is difficult to ascertain. Indeed, it is notable that this genus lacks all other hypothesized derived characters synapomorphous for the Citharinidae and Distichodontidae.

Within the African Characidae the hypothesized plesiomorphous posterior position of the bulb has been found in *Micralestes* (*M. acutidens*, *M. lualabae*, *M. voltae* and *M. occidentalis*), *Phenacogrammus interruptus*, *Rhabdalestes tangensis*, *Virilia pabrensis* and some *Alestes* species (*A. sadleri* and *A. longipinnis*). A slight separation between the bulb and telencephalon is found in *Alestes lateralis* and *A. imberi*, and the bulb has a distinct anterior shift in *Hydrocynus*, *Bryconaethiops* and a variety of *Alestes* species (*A. dentex*, *A. baremose*, *A. liebrechstii*, *A. macrophthalmus*, *A. macrolepidotus*, *A. nurse* and *A. rhodopleura*). This progressive anterior movement in the position of the olfactory bulb within a group that forms a monophyletic unit within the Characidae (see p. 341) was evidently acquired independently of that in citharinids and distichodontids. Finally, within the Parodontidae a slight forward shift of the bulb has been found in *Parodon bimaculatus* and *Apareidon affinis*. The significance of the Parodontidae in the question of the relationships of the families under discussion is reviewed later.

Phylogenetic reconstruction

The preceding descriptions of various osteological and soft anatomical systems have discussed a series of characters providing information relevant to a reconstruction of a hypothesis of generic relationships within the assemblage consisting of the Citharinidae and Distichodontidae. The following discussion deals first with the synapomorphies for the complex formed by citharinids and distichodontids, followed by those derived characters that distinguish subunits of decreasing levels of universality within this assemblage. The resultant phylogeny and its implication for the classification of these families is discussed subsequently.

The most parsimonious hypothesis of relationships based on the derived characters analysed previously is presented in Fig. 47. The apomorphous characters defining the genera and supra-generic assemblages are numbered sequentially, since such a procedure simplifies the visualization of character distribution and generic relationships. The numbering of the characters corresponds to the numbered synapomorphies of the cladogram in Fig. 47. Relationships at the subgeneric level are discussed in detail for only five of the taxa recognized in this study (*Neolebias*, *Ichthyborus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax*) in so far as the conclusions reached in this work are congruent with or at least fail to refute the hypotheses of relationships inherent in the previous definitions of the remaining genera. The characters synapomorphous for subgeneric units in *Neolebias* and *Ichthyborus* are incorporated into the cladograms presented in Fig. 48 and 49.

Families Citharinidae and Distichodontidae

The hypothesized monophyly of the assemblage formed by the Citharinidae and Distichodontidae is supported by the following synapomorphies of these families:

1 the ventral elaborations of the second and third vertebrae and the ventral expansion of the os suspensorium.
2 the bicuspidate tooth form.
3 the fusion of postcleithra 2 and 3.
4 the bifurcate pelvic bone.
5 the fusion of hypurals 1 and 2.
6 the lack of a premaxillary ascending process.
7 the possession of a premaxillary articular fossa.
8 the lack of lateral supraethmoid wings.
9 the lack of a distinct supraethmoid spine.
10 the trifurcate articular complex at the anterior margin of the supraethmoid.
11 the large, ventrally ovate third posttemporal fossa bordered by the epioccipital and exoccipital.
12 the anterior shift of the olfactory lobe.
13 the possession of a suprapreopercle.
14 the lack of an interdigitating symphyseal hinge.

As discussed in the anatomical descriptions, some of the above characters are evidently unique to these families among characoids, whereas others are approximated in characoid outgroups. On the basis of available information, the first four characters would appear to be autapomorphous for the unit formed by the Citharinidae and Distichodontidae among characoids. Characters similar to five to twelve occur in other characoid groups. However, available evidence indicates that their presence in these outgroups is a consequence of convergence rather than the result of immediate common ancestry. Finally, characters 13 and 14, though hypothesized as derived, also occur in characoid groups whose affinities are uncertain at present and thus are possibly sister groups to the unit consisting of citharinids and distichodontids. In addition to the characters listed above, it should also be noted that citharinids and distichodontids have a straight lateral line and an elongate posterior swimbladder chamber, characters whose polarity is, however, presently undetermined.

Within the hypothesized monophyletic assemblage defined by the characters detailed above, two families, the Citharinidae and Distichodontidae, are recognized in this study. Citharinids

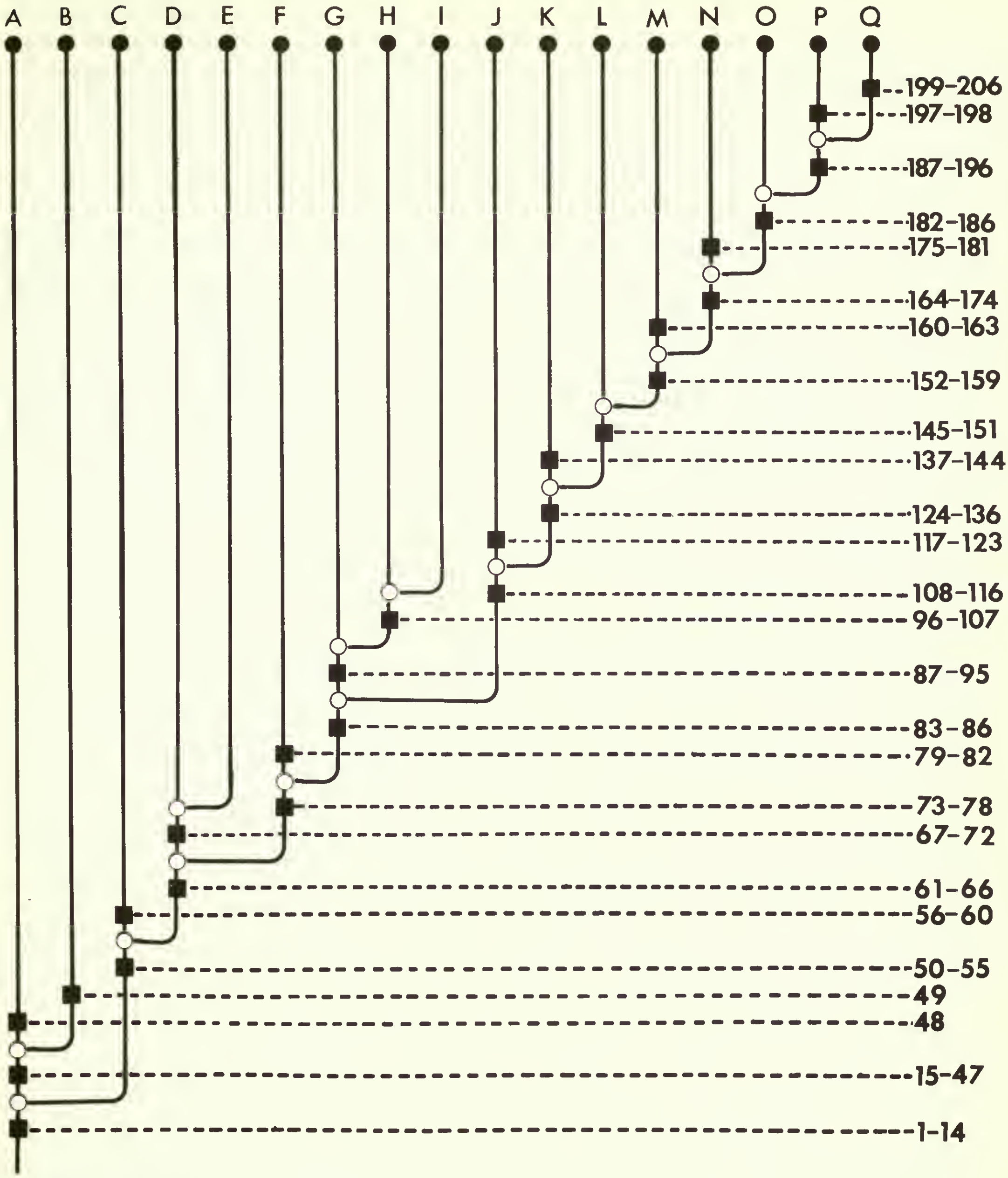
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Fig. 47 Cladogram of the most parsimonious hypothesis of relationships in the families Citharinidae and Distichodontidae. Taxa (solid circles): A, *Citharidium;* B, *Citharinus;* C. *Xenocharax;* D, *Nannaethiops;* E, *Neolebias;* F, *Paradistichodus;* G, *Distichodus;* H, *Nannocharax;* I, *Hemigrammocharax;* J, *Hemistichodus;* K, *Ichthyborus;* L, *Microstomatichthyoborus;* M, *Mesoborus;* N, *Eugnatichthys;* O, *Paraphago;* P, *Phago;* and Q, *Belonophago*. Synapomorphies 1–206 correspond to those of the text.

are a highly specialized group characterized by a series of distinctive synapomorphies, but having little intrafamilial variation. Indeed, the differences between citharinid species are primarily meristic and morphometric other than for the single character autapomorphous for each of the contained genera. In contrast, the Distichodontidae, although characterized by few synapomorphies, is very speciose and exhibits a pronounced degree of intrafamilial variation. The significance of these diametrically opposed trends in citharinids and distichodontids is obscure and indeed may only be a function of the differing speciation and extinction rates in these families as viewed at this particular point in time.

Family Citharinidae

As mentioned above, the family Citharinidae is distinguished by a multitude of apomorphous characters. The derived features of citharinids are nearly all related to the pronounced restructuring of the pars sustentaculum and the alterations in their ingestive and digestive systems correlated with their microphagous habits. These characters, in summary, are:

15 the marked expansion of the ventral processes of the second and third vertebrae and os suspensorium.
16 the independent ossification along the anterior and lateral surfaces of the coeliac sheath.
17 the outwards rotation of the replacement tooth trenches, particularly that of the lower jaw.
18 the posterior extension of the premaxilla medially, and the associated development of strong interpremaxillary interdigitations.
19 the ontogenetic reduction in the roof of the premaxillary fossa.
20 the reduction of the maxilla.
21 the loss of maxillary teeth.
22 the loss of the inner dentary tooth row.
23 the enlarged cartilage pad between the palatine and maxilla.
24 the development of a large cartilage pad between the palatine and premaxilla.
25 the ontogenetic reduction of the lateral articular processes of the supraethmoid and their fusion with the enlarged median supraethmoid process.
26 the restructuring of the lower pharyngeal into a fenestrated, dorsally convex, edentulous bone.
27 the fusion of upper pharyngeal tooth plates 4 and 5, and the reduction or loss of the associated dentition.
28 the loss of pharyngobranchial 1.
29 the elongation and anterior shift of pharyngobranchials 2 and 3.
30 the possession of micro-gillrakers.
31 the large, elaborate epibranchial organ.
32 the pronounced flexure in the parasphenoid.
33 the ontogenetic development of a bulbous ventral parasphenoid process.
34 the two broad regions of contact between the lateral ethmoid and orbitosphenoid.
35 the prominent, horizontal bulge at the orbitosphenoid–pterosphenoid joint.
36 the loss of the dorsal posttemporal fossa.
37 the elongate fontanelle extending midway into the supraethmoid.
38 the prominent ridge on the elongate anterodorsal process of the opercle.
39 the extension of the suprapreopercle over the anterodorsal portion of the opercle.
40 the reduced dermosphenotic.
41 the expansion of the dilatator fossa onto the frontal.
42 the attachment of the lateral section of the A_2 portion of the *adductor mandibulae* onto the A_W.
43 the relative reduction of the A_3 portion of the *adductor mandibulae*.
44 the enlargement of the A_W portion of the *adductor mandibulae* into a large muscle extending dorsal of the edge of the angulo-articular.
45 the marked enlargement of the *dilatator operculi*.

46 the elongation of the intestinal tract.
47 the pronounced outpocketings of the terminal portion of the intestine.

Within citharinids, two genera, *Citharinus* and *Citharidium*, are recognized at present. As described previously, the form of the ctenoid scales in *Citharidium* (48) appears to be unique among characoids to this monotypic genus. Traditionally, *Citharinus* has been distinguished from *Citharidium* on the basis of the former taxons having cycloid scales. However, such a scale form is plesiomorphous for characoids and thus cannot serve to define a monophyletic group. The only autapomorphous character for *Citharinus* found during this study is its lack of the parietal portion of the supraoccipital sensory canal (49). Such a loss, which appears to be derived for characoids, was previously noted by Daget (1962*b*, p. 95). Daget has also dealt with the ecology and aspects of the anatomy and taxonomy of both *Citharinus* and *Citharidium* (1962*a* & *b*).

Family Distichodontidae

As defined in this study the family Distichodontidae is both the most speciose and morphologically diverse of the families under consideration. Perhaps as a consequence of these factors, the Distichodontidae was previously subdivided into four subfamilies by Eigenmann (1909) and Regan (1911). More recently two subfamilies (Distichodontinae and Ichthyborinae) or families (Distichodontidae and Ichthyboridae) have been recognized within this assemblage. However, as will be discussed in the Conclusions section, the results of this study have led to the retention of only a single family, the Distichodontidae, for the genera previously partitioned among several subfamilies or families.

Despite this extensive intrafamilial variation, the Distichodontidae is not characterized by a large series of synapomorphous characters. The derived characters supporting the hypothesized monophyletic nature of the family Distichodontidae are:

50 the distinctive ctenoid scales having the ctenii formed by a series of independent ossifications.
51 the posterior process of the lateral ethmoid which extends posteriorly to contact the anteromedial edge of the orbitosphenoid.
52 the deeply bifurcate pelvic bone.
53 the mobility of the premaxilla on the supraethmoid.
54 the anterior shift and reduction or loss of the supraorbital.
55 the attachment of the A_1 portion of the *adductor mandibulae* to the maxilla (this attachment is secondarily lost in some genera, see p. 320).

These apomorphous characters define an assemblage of genera that is, in turn, divisible into two monophyletic subgroups. One unit consists of the genus *Xenocharax*, and the other of *Nannaethiops*, *Neolebias*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

In terms of overall body form, myology, osteology and dentition, *Xenocharax* is the least derived member of the monophyletic unit formed by citharinids and distichodontids. This generalized morphology is reflected in the omnivorous diet of this monotypic genus (see Daget, 1960, p. 39). Although characterized by a generalized morphological plan, the genus, nonetheless, possesses a series of apomorphous characters, some of which are unique to *Xenocharax* among characoids examined. These adaptations include:

56 the posterodorsal shift of the longitudinal axis of the vertebrae of the pars sustentaculum.
57 the marked reduction in the angle between the axis of the pars sustentaculum and the axis of the os suspensorium.
58 the subdivision of the suprapreopercle into two bony tubes.
59 the reduction in the branchiostegal number to three.
60 the increase to two inner dentary tooth rows.

Further information on the anatomy, biology and distribution of this genus is provided by Daget (1960).

The subunit of distichodontids formed by *Nannaethiops*, *Neolebias*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* has a series of synapomorphies involving alterations to the pterotic and dermosphenotic and their associated sensory canals, together with adaptations of the neurocranium and opercle. The synapomorphous characters shared by these genera are:

61 the posterior expansion of the dermosphenotic over the primitively exposed lateral surface of the pterotic.
62 the shift of the contact of the suprapreopercle to the dermosphenotic.
63 the elaboration of the plesiomorphously Y-shaped dermosphenotic sensory canal system into an H-shaped complex.
64 the decrease in the laterally exposed portion of the pterotic and the reduction of the pterotic sensory canal system to a simple tube.
65 the possession of some form of fenestrated opercle.
66 the reduction of the cranial fontanelle so that it barely extends anterior of the epiphyseal bar.

Two subunits of the assemblage defined by characters 61–66 can in turn be distinguished by their less universal apomorphous characters. The first subunit is formed by the genera *Nannaethiops* and *Neolebias*, while the second consists of *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The complex formed by the genera *Nannaethiops* and *Neolebias* (the latter in this sense is equivalent to *Neolebias*, *Congocharax* and *Dundocharax* of previous authors) can be defined by the following derived characters:

67 the expansion of the suprapreopercle into a flat plate fitting the posteroventrally concave dermosphenotic.
68 the loss of the suprapreopercular sensory canal segment.
69 the marked secondary reduction or loss of the lateral ethmoid process extending between the lateral ethmoid and orbitosphenoid.
70 the reduction or loss of the portion of the dermosphenotic sensory canal communicating with the suprapreopercular sensory canal.
71 the possession of a ectopterygoid tooth patch.
72 the loss of the sixth hypural.

Among the distichodontid genera with several species, the complex formed by *Nannaethiops* and *Neolebias* is undoubtedly the best understood at the alpha-level. In their revision of these genera, Poll & Gosse (1963) dealt with all of the then known species in addition to describing several new forms. More recently Matthes (1964) described a new species, *Neolebias gracilis*. In the same publication that author removed *N. spilotaenia* to the genus *Congocharax* along with *C. olbrechtsi* which previously had been included in *Hemigrammocharax*. Poll & Lambert (1964), in turn, described a new species, *Congocharax gossei*, and Poll (1967) erected the genus *Dundocharax* for *D. bidentatus* which he described at the same time. Both *Congocharax* and *Dundocharax*, however, share the distinguishing characters of *Neolebias* and as will be discussed are placed into synonymy of that genus.

The cladogram of Fig. 48 shows the hypothesized interrelationships of *Nannaethiops* and *Neolebias* species based on evidence of this study. Characters uniting *Neolebias* and the monotypic genus *Nannaethiops* into a monophyletic unit were discussed above. Apomorphous characters common to subunits of this assemblage are:

(A) the reduction of the lateral line.
(B) the reduction or loss of the posteroventral and posterodorsal segments of the dermosphenotic sensory canal segment.
(C) the loss of one of the infraorbitals at the posterior margin of the orbit.
(D) the shift of the remaining infraorbitals so as to retain a fully ossified orbital rim.
(E) the total loss of the sensory canal systems of the dermosphenotic and pterotic.
(F) the loss of the remaining infraorbital element at the rear of the orbit.

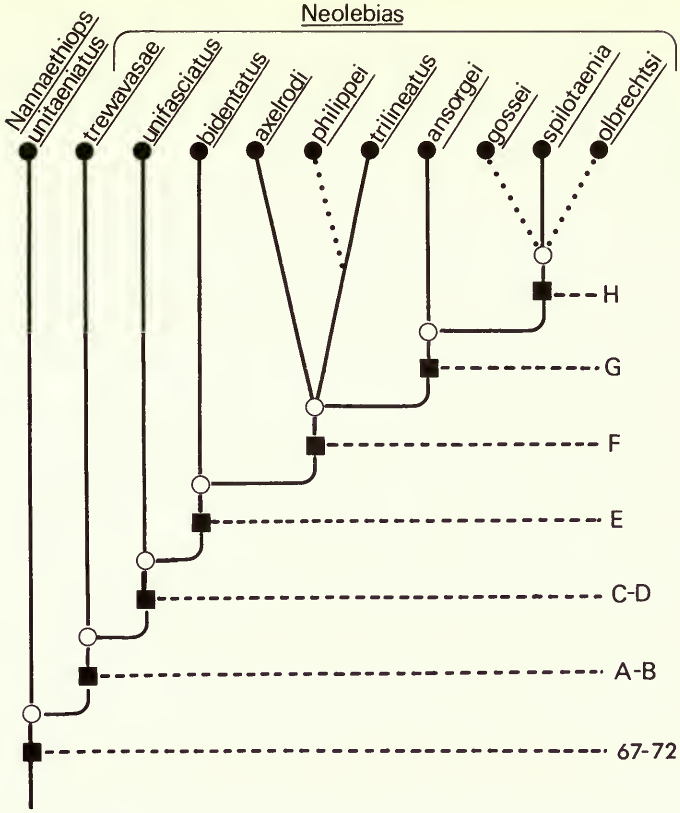

Fig. 48 Cladogram of the most parsimonious hypothesis of relationships in the unit formed by the genera *Nannaethiops* and *Neolebias*. Synapomorphies A–H correspond to those of the text.

(G) the loss of the dermosphenotic.

(H) the distinctive sensory pore system of the head.

Relationships of those species whose hypothesized phylogenetic position is based solely on information from the literature is indicated by dotted lines. *Neolebias phillipei*, as noted by Poll & Gosse (1963), appears to be closely related to *N. trilineatus* with which it shares an increased number of body stripes, a reduced circumpeduncular scale series and a low transverse scale count. *Neolebias olbrechtsi* and *N. gossei* share with *N. spilotaenia* a distinctive cranial sensory pore pattern which is unique to these species among distichodontids (see Poll & Lambert, 1964*b*, p. 407). Whether the former species also have *N. spilotaenia's* distinctive gill arch modifications and loss of infraorbitals 2 and 3 awaits further study. *Neolebias gracilis* of Matthes (1964) cannot be more closely assigned on the basis of literature information. However, it is difficult to visualize how the characters of this species could drastically alter the phylogeny arrived at here. The most parsimonious phylogeny resulting from the described characters necessitates several modifications to the previous taxonomy of species placed in *Neolebias* as a result of this study.

Neolebias bidentatus was originally placed by Poll (1967, p. 129) in the genus *Dundocharax* which was described at the same time. Despite Poll's statement that 'Ce genre est voisin du genre *Hemigrammocharax* . . .', the evidence now available shows it to belong to *Neolebias* as defined in this study. In addition to having the various characters autapomorphous for *Neolebias* among distichodontids, *Dundocharax* also lacks the multitude of apomorphous characters uniting *Hemigrammocharax* to *Nannocharax* and *Distichodus*. *Neolebias spilotaenia*, *N. gossei* and *N. olbrechtsi*, in turn, were placed in *Congocharax* by Matthes (1964) and Poll & Lambert (1964) on the basis of their distinctive cranial sensory pore patterns. Although available evidence supports the hypothesis of the monophyletic nature of the unit formed by these three species, it also indicates that they are assignable to the genus *Neolebias* as defined herein. Although both *Congocharax* and *Dundocharax* from monophyletic subunits of the Distichodontidae (the latter by virtue of its monotypy), reference to the cladogram in Fig. 48 shows that the recognition of both *Dundocharax* (*Neolebias bidentatus*) and *Congocharax* (*N. spilotaenia*, *N. olbrechtsi* and *N. gossei*) as separate genera would result in *Neolebias* (*sensu stricto*) being a non-monophyletic assemblage. This is a consequence of the fact that *Neolebias* is such a sense would not contain all descendants of its hypothesized common ancestor. In light of this inconsistency with a basic taxonomic principle of this study, and in so far as a uniqueness criterion for the determination of generic rank is arbitrary, both *Dundocharax* and *Congocharax* are placed as synonyms of *Neolebias*. *Neolebias* in this broader sense now constitutes a monophyletic subunit of the Distichodontidae.

A difference between the findings of this study and published observations should also be noted. Matthes in his diagnosis of the genus *Congocharax* (1964, p. 76) stated that it has the 'Maxillaire non denté . . .', a statement repeated by Poll & Lambert (1964, p. 336). However, this comment is contrary to the observed presence of three or four maxillary teeth throughout the type series of *Neolebias spilotaenia* (the *Congocharax spilotaenia* of the above workers). Furthermore, it conflicts with Poll & Gosse's statement that this species is characterized by 'Présence de dents a l'angle supérieur de maxillaire.' Whether the reported absence of teeth in *Neolebias gossei* and *N. olbrechtsi* is correct awaits further study. [Since this paper has gone to press, I have had the opportunity to examine specimens of *N. olbrechtsi*. That species has two bicuspidate maxillary teeth and derived characters 1–72 and A–H for *Neolebias*.]

The sister group to the unit formed by *Nannaethiops* and *Neolebias* is the multigeneric assemblage consisting of *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera share a series of synapomorphous jaw and suspensorium modifications including:

73 the lengthening of the horizontal extent of the suspensorium with a resultant forward shift of the articulation between the angulo-articular and quadrate.
74 the pronounced expansion of the premaxillary and dentary replacement tooth trenches.
75 the distinct horizontal shelf on the lateral surface of the quadrate and preopercle.
76 the loss of maxillary teeth.
77 the elongation of the teeth in the outer tooth row of each jaw and their pleurodont attachment to the anterior surface of the replacement tooth trench.
78 the possession of a distinct opercular fenestra.

The subunit of the Distichodontidae defined by these characters is, in turn, divisible into two monophyletic subunits. The first of these consists solely of the genus *Paradistichodus*, whereas the second contains *Distichodus*, *Hemigrammocharax*, *Nannocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The genus *Paradistichodus* contains two species characterized by the following hypothesized apomorphous characters:

79 the reduction in the number of hypurals to five.
80 the elongation of the supraethmoid.
81 the reduction in the number of epurals to one.
82 the reduction of the muscular portion of the lateral section of the A_2 portion of the *adductor mandibulae*.

Daget (1958) has discussed the biology, and aspects of the anatomy of the two nominal *Paradistichodus* species, *P. elegans* from the Chad and Benue systems and *P. dimidiatus* from the Niger and Gambia drainages. However, as discussed by Daget the differences between these nominal species are slight and may be a function of geographic variation.

The assemblage consisting of *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is characterized by the following hypothesized apomorphous characters:

83 the mobile articulation of the angulo-articular with the dentary.

84 the increased mobility of the upper jaw on the supraethmoid.
85 the increased attachment of the mesopterygoid to the neurocranium.
86 the increased envelopment of the palatine by the ectopterygoid and mesopterygoid.

The two subunits definable within the group of genera sharing characters 83 to 86 are the speciose assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, and the multigeneric unit consisting of *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The hypothesized monophyletic group consisting of *Distichodus*, *Nannocharax* and *Hemigrammocharax* forms a very distinctive unit within distichodontids on the basis of a series of apomorphous characters, some of which are unique to this assemblage within characoids. These characters are:

87 the pronounced restructuring of the overall form of the dentary and the anteroventral reorientation of its longitudinal axis.
88 the reduction or loss of the sensory canal segment in the dentary.
89 the anterior restructuring of the angulo-articular into an anterodorsally or dorsally-directed plate.
90 the marked overlap of the dentary and angulo-articular.
91 the elongation of the outer row of premaxillary and dentary teeth.
92 the reduction or loss of the anteromedial process of the supraethmoid.
93 the dorsal shift of the insertion of the lateral section of the A_2 portion of the *adductor mandibulae*.
94 the origin of the A_W portion of the *adductor mandibulae* from the dorsal edge of the tendon of the A_2 and A_3 sections of the muscle, and the pronounced extension of the A_W posterior of the edge of the angulo-articular.
95 the crossing at right angles of the *ligamentum primordiale* and the tendon of the A_1 portion of the *adductor mandibulae*.

These characters are all either modifications of the jaws, or osteological and myological alterations correlated with the distinctive jaws and jaw action of these genera. Functionally, these alterations have resulted in a system permitting a degree of horizontal dentary motion that is unique among characoids.

Within the hypothesized monophyletic assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, a subunit consisting of *Nannocharax* and *Hemigrammocharax* is definable on the basis of the following synapomorphies:

96 the posteriorly-directed dentary processes flanking the dentary symphysis.
97 the loss of the inner premaxillary tooth row.
98 the loss of the sensory canal segment in the dentary.
99 the loss of the inner dentary tooth row.
100 the reduction or loss of the premaxillary articular fossa.
101 the vertical expansion of the posterior strut of the lateral ethmoid.
102 the horizontal expansion of the hyomandibula.
103 the loss of postcleithrum 1.
104 the development of anterior diverticulae of the anterior swimbladder chamber.
105 the restructuring of the ventral portion of the sphenotic spine into a posteroventrally sloping shelf.
106 the opening of the opercular fenestra to the dorsal margin of the bone.
107 the reduction of the metapterygoid–quadrate fenestra.

Although both the assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, and the unit consisting of *Nannocharax* and *Hemigrammocharax* are defined by a series of apomorphous characters, the monophyly of the genera *Distichodus*, *Hemigrammocharax* and *Nannocharax* is either refuted or brought into question by the results of this study. Previous classifications utilized the larger size, higher dorsal fin-ray count and multiple rows of functional premaxillary and dentary teeth of *Distichodus* as the main characters distinguishing that genus from the unit formed by *Nannocharax* and *Hemigrammocharax*. However, in so far as all citharinids and distichodontids are larger as adults than *Nannocharax* and *Hemigrammocharax* species, the larger size of *Distichodus* species relative to that of these genera appears to be plesiomorphous. Similarly, the high dorsal-fin ray count and inner row of premaxillary and dentary teeth are widespread among distichodontids (the former feature also occurs in citharinids). Thus both of these characters must be considered plesiomorphous for the group formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*. Consequently none of the characters previously used as distinguishing features of *Distichodus* relative to *Nannocharax* and *Hemigrammocharax* is a valid basis for a hypothesis of the monophyly of *Distichodus*. Furthermore, none of the apomorphous characters found during this study support such a hypothesis. Indeed the results of this investigation indicate that as presently constituted *Distichodus* represents a grade level concept, with some *Distichodus* species more closely related to the unit formed by *Nannocharax* and *Hemigrammocharax* than to their congeners. The characters refuting the hypothesis of the monophyly of *Distichodus* are:

(A) the restructuring of the articular processes of the supraethmoid into pointed prong-like structures in *Distichodus lusosso*, *D. niloticus* and *D. fasciolatus*. This approximates to the hypothesized derived *Nannocharax* and *Hemigrammocharax* forms of these structures, but contrasts with the plesiomorphous flattened condition of the processes in *Distichodus notospilus* and *D. brevipinnis*.

(B) the elongation of the supraethmoid in *Distichodus lusosso*, *D. niloticus* and *D. fasciolatus*. This feature is shared with *Nannocharax* and *Hemigrammocharax* but contrasts with the plesiomorphous square supraethmoid in some *Distichodus* species.

(C) the shift from the transversely elongate articular fossa on the rear of the premaxilla present in *Distichodus notospilus* and *D. brevipinnis* to a dorsally located pit in *D. lusosso*, *D. niloticus* and *D. fasciolatus*. The latter condition approximates to the derived articular fossa form of *Nannocharax* and *Hemigrammocharax*.

(D) the ventral expansion of the sphenotic spine in *Distichodus lusosso* and *D. niloticus*, a modification carried further in *Nannocharax* and *Hemigrammocharax*. This condition contrasts with the plesiomorphous ventrally sharp-edged spine common to some *Distichodus* species.

These characters and associated changes in neurocranial form are congruent with the hypothesis that *D. lusosso*, *D. niloticus* and *D. fasciolatus* are more closely related to the unit formed by *Nannocharax* and *Hemigrammocharax* than to some of their congeners. It is thus concluded that the genus *Distichodus* as presently defined is non-monophyletic. However, the exact distribution of these and other derived characters among the numerous nominal *Distichodus* species awaits further study as does a redefinition of *Distichodus* based on derived characters.

As discussed previously *Nannocharax* and *Hemmigrammocharax* share a multitude of apomorphous characters congruent with the hypothesized monophyly of the unit they form within distichodontids. However, the monophyly of each of these genera is open to question. Previous classificatory schemes differentiated these genera on the basis of the reduced lateral line in *Hemigrammocharax*, in contrast to the retention of the plesiomorphous complete lateral line in *Nannocharax*. However, although it is most parsimonious to assume that a reduced lateral line is derived within distichodontids, as discussed by Roberts (1967, p. 252) there is some doubt as to whether the reduced lateral line of the various *Hemigrammocharax* species results from common ancestry or multiple independent losses. Furthermore, the distribution of derived states of the infraorbital series, fourth upper pharyngeal tooth plate and ossifications of the submaxillary cartilage are incongruent with the hypothesis of the monophyletic nature of both *Nannocharax* and *Hemigrammocharax* as presently defined.

A resolution of the question of the monophyletic nature of the genera *Nannocharax* and *Hemigrammocharax* and of the relationships within the complex formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax* would necessitate a total revision of this speciose assemblage. Such an undertaking is beyond the aim of this study. Thus, until such a study is accomplished, these genera are tentatively retained as presently defined although the hypothesis of the monophyly of *Distichodus* is contraindicated and that of *Nannocharax* and *Hemigrammocharax* cast in doubt. Further information on the ecology, anatomy and taxonomy of some *Distichodus* and *Nannocharax* species can be found in Daget (1959, 1961).

The sister group to the assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax* consists of the genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera form a distinctive subunit of distichodontids sharing the following derived characters:

108 the marked reduction of the maxilla.
109 the loss of the medially-directed anterodorsal maxillary process.
110 the immovable articulation between the maxilla and premaxilla.
111 the prominent posterodorsal dentary process.
112 the elongation of the metapterygoid–quadrate fenestra and an increased contribution of the symplectic to its posterior border.
113 the markedly increased upper jaw mobility.
114 the medial shift of the position of the preopercular sensory canal.
115 the loss of the attachment of the A_1 portion of the *adductor mandibulae* to the maxilla.
116 the strongly developed teeth of the outer tooth row.

The above adaptations are primarily associated with the functionally distinctive jaws characteristic of these genera. As noted earlier, the loss of the attachment of the A_1 portion of the *adductor mandibulae* to the maxilla is considered an apomorphous secondary loss for this assemblage. Among other distichodontids such an attachment is advantageous in contributing to the greater mobility of the upper jaw. However, the restructuring of the jaws in the genera under discussion results in a pronounced motion of the upper jaw without the necessity for an insertion of the A_1 on the maxilla. Indeed, in these genera the retention of such an attachment would be ineffective or of little advantage due to the drastically altered form of the maxilla and its immobile articulation with the premaxilla.

Within the assemblage defined by apomorphies 108–116, two monophyletic subunits are distinguishable on the basis of shared derived characters. These are the genus *Hemistichodus* and the unit formed by *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The members of the genus *Hemistichodus* are distinguished by a series of jaw and dental modifications, most of which are unique among characoids examined. The apomorphies for the genus are:

117 the greatly reduced maxilla which is totally excluded from the gape.
118 the pronounced development of the posterodorsal dentary ramus.
119 the great reduction and restructuring of the supraethmoid.
120 the modification of the premaxillary articular fossa into a rounded depression on the dorsal surface of the bone.
121 the loss of the inner tooth row on the dentary and premaxilla.
123 the lateral orientation of the replacement tooth trenches.

Hemistichodus consists of three west African and Congo basin species which have a relatively small adult size. Within the genus, *Hemistichodus mesmaekersi* and *H. lootensi* are hypothesized to form a monophyletic group on the basis of their apomorphous medially interrupted lateral line (see Daget, 1968, Fig. 1). These species, in turn, constitute the sister group to the third *Hemistichodus* species, *H. vaillanti*. Daget (1968) has reviewed aspects of the anatomy, biology and taxomony of the members of *Hemistichodus*.

The sister group to *Hemistichodus* within the Distichodontidae is formed by the assemblage consisting of *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera have a series of synapomorphous modifications of the jaws, neurocranium and dermal head bones including:

124 the loss of the posteroventral process of the dentary.
125 the reduction of the infraorbital series to four elements.
126 the interdigitating premaxillary joint or a further derived condition of such a symphysis.
127 the horizontal elongation of the sphenotic and the reorientation of the sphenotic spine into a posteroventrally sloping or horizontal shelf having a reduced lateral extent.
128 the loss of the lateral ridge on the lateral commissure and on portions of the sphenotic and parasphenoid.

129 the reduced contribution of the prootic to the lip of the opening to the posterior myodome.
130 the transverse ridge on the ventral surface of the frontal.
131 the posterior shift of the hyomandibular fossa and lateral commissure.
132 the slender, anteriorly concave hyomandibular.
133 the reduction of the cranial fontanelle to posterior to the epiphyseal bar.
134 the lateral and posterior expansion of the horizontal shelf on the lateral surface of the preopercle.
135 the expansion of the origin of the *adductor mandibulae* onto the medial face of the hyomandibula and lateral surface of the sphenotic and pterotic.
136 the expansion of the origin of the *levator arcus palatini* onto the anterior surface of the sphenotic spine.

These modifications, which are primarily related to the jaws and jaw action, result in a lower jaw motion unique to these genera among characoids (see p. 271). Within this assemblage a dichotomous sister group relationship is hypothesized between *Ichthyborus* (the *Ichthyborus*, *Phagoborus* and *Gavialocharax* of previous authors) and the multigeneric unit consisting of *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The genus *Ichthyborus* as herein defined is a distinctive assemblage of four species characterized by the following synapomorphous characters:

137 the symphyseal fusion of the dentaries.
138 the enlargement of the anterior tooth cusp.
139 the possession of a median dentary tooth.
140 the form of the angulo-articular-dentary joint.
141 the posterodorsal expansion of infraorbital 4 and the congruent separation of the dermosphenotic from the orbital rim.
142 the marked median shift of the preopercular sensory canal segment in the vertical portion of the bone.
143 the loss of the ligamentous attachment of the palatine to the maxilla.
144 the insertion of the A_1 portion of the *adductor mandibulae* on the angulo-articular.

Together these adaptations result in a distinctive subunit of distichodontids specialized for an ichthyovorous diet, although one subspecies of *Ichthyborus besse* is reported to be a fin eater (see Lek & Lek, 1978). The taxonomic concept of *Ichthyborus* in this work is, however, much broader than that of earlier workers. Figure 49 illustrates the hypothesized relationships of the four species assigned to *Ichthyborus* in this study. The characters synapomorphous for *Ichthyborus* were discussed above. Apomorphous characters common to subunits of this genus are:

(A) the greater relative enlargement of the anterior tooth cusp.
(B) the enlarged canine-like teeth at the front of each jaw.
(C) the loss of the inner dentary tooth row.
(D) the loss of the inner premaxillary tooth row.
(E) the elongation of the jaws.

Previous classifications placed *Ichthyborus monodi* and *I. besse* in the monotypic genera *Gavialocharax* and *Ichthyborus* respectively, whereas *I. ornatus* and *I. quadrilineatus* were assigned to *Phagoborus*. However, in light of the phylogeny arrived at here, such a subdivision is untenable since in such a system *Phagoborus* (the *I. ornatus* and *I. quadrilineatus* of this study) does not form a monophyletic unit. In order to resolve this inconsistency both *Phagoborus* and *Gavialocharax* are synonymized with *Ichthyborus*. This results in *Ichthyborus* (*sensu lato*) forming a monophyletic multispecific subunit of distichodontids. In contrast, the alternative possibility, the erection of a new genus to contain *I. quadrilineatus*, fails to indicate the relationship of its sole species to other members of this complex and further subdivides an already greatly split assemblage.

Finally, a discrepancy between the findings of this study and published information should be noted. Pellegrin (1904) and Boulenger (1909) described *Ichthyborus quadrilineatus* (the *Neoborus quadrilineatus* of those authors) as having a single series of teeth in each jaw. However, in all *I. quadrilineatus* specimens examined an inner row of premaxillary teeth is also present.

The genera *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* are hypothesized as forming a monophyletic unit on the basis of their common possession of the following derived characters:

145 the enlargement of the posterior tooth cusp.
146 the possession of an immobile interdigitating joint at the rear of the dentary symphysis.
147 the anterior and posterior expansion of the third infraorbital.
148 the form of the angulo-articular-dentary articulation.
149 the loss of the supraorbital.
150 the reduction of the anteromedial supraethmoid process.
151 the possession of a posterodorsal preopercular flange.

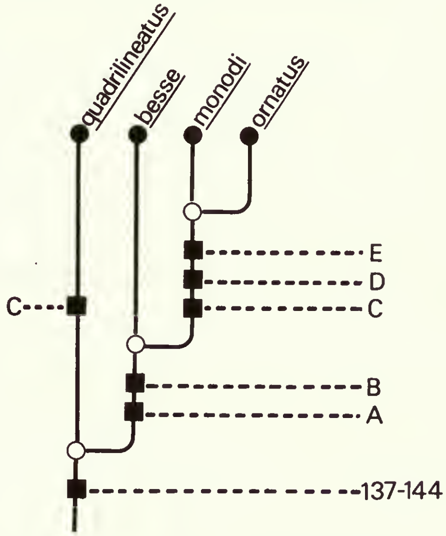

Fig. 49 Cladogram of the most parsimonious hypothesis of relationships in the genus *Ichthyborus*. Synapomorphies A–E correspond to those of the text

Within the subunit of distichodontids defined by apomorphous characters 145–151, a dichotomy is hypothesized between *Microstomatichthyoborus* and the group formed by *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. However, whereas the latter genera share a series of apomorphous characters, no derived feature unique to *Microstomatichthyoborus* in the Distichodontidae has been found in this study. Nonetheless, because of the lack of evidence contraindicating the monophyly of the unit formed by the two nominal *Microstomatichthyoborus* species (*bashforddeani* and *katangae*), the genus is retained for the present.

The genera *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in contrast, share the following apomorphous characters:

152 the reorientation of the sphenotic spine into an horizontal shelf.
153 the lateral reduction of the sphenotic spine so as to barely reach laterally to the frontal.
154 the loss of the cartilaginous rod joining the palatine to the maxilla.
155 the pronounced reduction of the laterally exposed portion of the pterotic and a shortening of the pterotic sensory canal.
156 the elongation of the pterosphenoid and orbitosphenoid.
157 the ventral shift of the attachment of the gill arches to the parasphenoid.
158 the pronounced reduction of the cranial fontanelle.
159 the presence of a fossa on the rear of the hyomandibula to receive the dorsal tip of the preopercle.

Characters 152–158 distinguish a generic assemblage which can in turn be divided dichotomously. One subunit consists of the genus *Mesoborus*, whereas the other is formed by the genera *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Mesoborus is a distinctive genus whose single contained species, *M. crocodilus*, is a voracious predator (Matthes, 1964, p. 65). This life style is reflected in the following autapomorphous modifications:

160 the ontogenetic loss of the anterior tooth cusp resulting in a nearly unicuspidate dentition.
161 the enlarged second to fourth dentary teeth.
162 the development of the anterior premaxillary teeth into canines.
163 the reduction of the second to fourth premaxillary teeth which arise from a distinctly concave region of the premaxilla.

The sister group to *Mesoborus* among distichodontids is formed by the genera *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This assemblage is characterized by the following apomorphies:

164 the transversely thickened and horizontally shortened angulo-articular.
165 the posteroventral recontouring of the maxilla into a rounded knob.
166 the development of a groove on the lateral surface of the posterodorsal dentary ramus.
167 the marked reduction of the anteromedial supraethmoid process.
168 the expanded, laterally-orientated supraethmoid articular processes.
169 the restructuring of the premaxillary articular fossa into a laterally directed pit.
170 the laterally reduced sphenotic spine which falls short of the edge of the frontal.
171 the reduction of the anterior sphenotic process capping the transverse ridge of the frontal.
172 the pronounced dorsal process of the hyomandibula.
173 the possession of a ventromedial parasphenoid ridge.
174 the reduction of the vertical extent of the *levator arcus palatini* and its attachment to the hyomandibula *via* an aponeurosis.

Most of these characters are either changes in the form of the jaws or alterations in their relationships to each other, the neurocranium and the suspensorium. These adaptations result in a close meshing of the upper and lower jaws during closure of the mouth. This tight fit together with the pronounced gape characteristic of these genera and their enlarged *adductor mandibulae* muscles results in a system well adapted for the fin-nipping habits previously reported for *Phago*, *Belonophago* and *Eugnatichthys* (see Matthes, 1961; Gosse, 1963; Burchard, 1968) and found in *Paraphago* during this study.

This assemblage of genera can, in turn, be dichotomously divided into two monophyletic subunits. These are the genus *Eugnatichthys* and the unit consisting of *Paraphago*, *Phago* and *Belonophago*.

Eugnatichthys is a distinctive genus of distichodontids characterized by the following autapomorphous characters:

175 the massive development of the premaxilla and dentary.
176 the transverse expansion of the maxilla.
177 the transversely expanded angulo-articular.
178 the subdivision of the A_3 portion of the *adductor mandibulae* muscle.
179 the horizontal elongation of the sphenotic, with an associated shift posteriorly of the lateral commissure and hyomandibular fossa.
180 the pronounced development of the median parasphenoid ridge into a knife-like process.
181 the reduction of the dorsal posttemporal fossa.

Eugnatichthys is composed of only two species (*eetveldii* and *macroterolepis*) but is one of the most distinctive genera among distichodontids as a consequence of its relatively massive jaws. These adaptations of the jaws and associated osteological systems, together with the pronounced development of the *adductor mandibulae* muscles, permit these species to bite off relatively thicker fin segments than can any other fin-eaters examined.

The hypothesized sister group to *Eugnatichthys* is formed by the unit consisting of *Paraphago*, *Phago* and *Belonophago*. This assemblage is characterized by the following hypothesized apomorphous characters:

182 the reduction or loss of infraorbital 4.
183 the expansion ventrally of the dermosphenotic.
184 the contact of the posteroventral border of the pterosphenoid with the ascending process of the parasphenoid.
185 the elongation of the jaws.
186 the loss of the anterior sphenotic process plesiomorphously capping the transverse ridge of the frontal.

It should be noted, however, that because *Paraphago* is known only from its syntypes, it was not possible to study the genus myologically, or to analyse those internal osteological characters not amenable to examination by radiographs. It is thus possible that some of the characters listed below as synapomorphies for *Phago* and *Belonophago* are shared with *Paraphago*. Although no characters autapomorphous for *Paraphago* within distichodontids were found during this study, the genus is, nonetheless, monophyletic by virtue of its monotypy.

The remaining distichodontid genera, *Phago* and *Belonophago*, share the following hypothesized synapomorphies:

187 the marked expansion of the supraethmoid articular processes into rounded, laterally-directed structures.
188 the extensive horizontal elongation of the symplectic, metapterygoid and metapterygoid–quadrate fenestra.
189 the loss of infraorbital 4.
190 the pronounced ventral expansion of the dermosphenotic.
191 the pronounced dorsal expansion of infraorbital 3.
192 the heavy bony scales having a prominent bump over the scale focus.
193 the single epural.
194 the very wide contact of the posteroventral margin of the pterosphenoid with the ascending process of the parasphenoid.
195 the ventral expansion of the fused postcleithra 2 and 3.
196 the expansion of the origin of the *levator arcus palatini* onto the ventral surface of the frontal.

Phago and *Belonophago* are, in turn, each characterized by several autapomorphous characters. Derived features of *Phago* are:

197 the thickened, vertically elongate scales.
198 the anteroventrally curved premaxilla that overlaps the anterior end of the dentaries.

Presently four nominal species of *Phago* (*boulengeri*, *intermedius*, *loricatus* and *maculatus*) occur in the literature. However, *P. maculatus* of the Niger drainage is questionably distinct from *P. loricatus* of the same system.

Belonophago is a very distinctive genus having the following autapomorphies:

199 the marked elongation of the jaws.
200 the expansion of the pterosphenoid so as to form the entire anterior surface of the braincase.
201 the median contact between the pterosphenoid and parasphenoid.
202 the extreme elongation of the metapterygoid and symplectic.
203 the loss of the sensory canal system in the dermosphenotic.
204 the loss of the sensory canal system in infraorbital 3.
205 the posteriorly-directed spinous processes on the scales.
206 the secondary loss of the transverse ridge on the ventral surface of the frontal.

The two nominal *Belonophago* species (*tinanti* and *hutsebouti*) are characterized by a markedly elongate, cylindriform shape (see Poll, 1957, Fig. 142). The fin-nipping habits of this genus were reported on by Matthes (1961, p. 78) and confirmed in this study by stomach content analyses.

Convergent characters

The hypothesis of relationships presented above is the most parsimonious derivable from available information on character distribution and polarity in the systems analysed among citharinids and distichodontids. However, as might be expected in such a large diverse assemblage, there occur a number of hypothesized apomorphous characters whose distribution is incongruent with that of the overall most parsimonious hypothesis of relationships. The majority of these incongruities are loss characters. Although loss characters provide useful information for a phylogenetic reconstruction, they can sometimes be misleading in so far as the non-homology of losses can be difficult to ascertain. Apomorphous loss characters which have a distribution incongruent with that of a majority of the derived characters among citharinids and distichodontids are:

(A) the loss of the maxillary teeth in citharinids and all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.

(B) the loss of the inner dentary tooth row in citharinids, *Hemistichodus*, some *Ichthyborus* species and the unit formed of *Nannocharax* and *Hemigrammocharax*.

(C) the loss of the inner premaxillary tooth row in *Hemistichodus*, some *Ichthyborus* species and the unit consisting of *Nannocharax* and *Hemigrammocharax*.

(D) the loss of the sixth hypural in *Paradistichodus* and the unit formed by *Neolebias* and *Nannaethiops*.

(E) the loss of one epural in *Paradistichodus* and the group consisting of *Phago* and *Belonophago*

(F) the loss of the cartilaginous connection between the palatine and maxilla in *Ichthyborus* and the assemblage containing *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

(G) the reduction of the anteromedian supraethmoid process in the group formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, and the unit consisting of *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

(H) the loss of the dermosphenotic sensory canal segment in some *Neolebias* species and the genus *Belonophago*.

(I) the reduction of the lateral line in *Neolebias* and *Hemigrammocharax*.

(J) the reduction of the maxilla in citharinids and the distichodontid genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Apomorphous gain characters evidently acquired independently several times in the assemblage formed by the Citharinidae and Distichodontidae are:

(A) the elongation of the jaws in some *Ichthyborus* species and the assemblage formed by *Paraphago*, *Phago* and *Belonophago*.

(B) the presence of a second inner dentary tooth row in *Xenocharax* and some *Neolebias trilineatus* specimens.

(C) the elongation of the supraethmoid in *Paradistichodus* and the unit consisting of *Nannocharax*, *Hemigrammocharax* and some *Distichodus* species.

(D) the interpremaxillary interdigitations of citharinids and the group formed by *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

In addition to the characters listed above there is also a series of apomorphies which although seemingly convergent within citharinids and distichodontids can, nonetheless, be shown to be non-homologous. Foremost among these is the loss of infraorbitals 4 and 5 in some *Neolebias* species, some *Nannocharax* species and the subunit of distichodontids formed by *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. As discussed earlier the loss of these bones in each of these groups is achieved by an independent non-homologous method. Similarly, the mode of reduction or loss of the metapterygoid–quadrate fenestra differs between *Neolebias spilotaenia* and the unit formed by *Nannocharax* and *Hemigrammocharax*. In the former the opening is eliminated by an expansion of the symplectic, whereas in the latter genera the fenestra is reduced or lost as a consequence of the approximation of the symplectic and metapterygoid. Similarly, the medially interrupted lateral line is *Hemistichodus* differs from the reduced lateral line of *Neolebias* and *Hemigrammocharax*. In the latter genera, the lateral line is lacking both medially and posteriorly with this reduction limited to the posterior part of the body in some *Hemigrammocharax* species (see *H. angolensis*, Poll, 1967, Fig. 51).

As noted earlier, the canine dentition of the lower jaws of *Mesoborus* and some *Ichthyborus* species differs in which teeth are enlarged. Although both of these taxa have the anterior teeth of the premaxilla enlarged, these canines are non-homologous. In *Mesoborus* the enlarged anterior premaxillary teeth are a consequence of the great expansion of the posterior tooth cusp. In *Ichthyborus*, in contrast, the canines are formed by an enlarged anterior cusp.

Finally, it should be noted that the differences between the reduced maxilla of citharinids and some distichodontids (loss character J) are such as to cast doubt in the homology of these reductions. Similarly, the interpremaxillary interdigitations occurring in citharinids and a subunit of distichodontids (gain character D) are rather different and may have arisen independently.

Thus many of the seemingly convergent characters are, on closer examination, found to be non-homologous. Even in those cases where the homology of the convergencies is not refuted, the overall distribution of apomorphous characters is such that any alterations made to the proposed phylogeny, in order to resolve some or all of these evident convergencies, results in a less parsimonious theory of interrelationships.

Conclusions

The translation of the proposed phylogeny into a classification has necessitated several major changes in the previous generic and suprageneric taxonomy of the genera herein assigned to the families Citharinidae and Distichodontidae. Most previous classifications (Boulenger, 1909; Monod, 1950; Greenwood *et al.*, 1966) recognize three families or subfamilies for this group of genera. Although the taxonomic level applied to any group of organisms is arbitrary, the familial level ranking of Greenwood *et al.*, which is most widely used in the modern literature, is retained.

The family Citharinidae of Greenwood *et al.* (1966) remains unchanged in so far as it was found to represent a monophyletic unit. In contrast, the previous concepts of the Distichodontidae (or subfamily Distichodontinae) included the genera *Xenocharax*, *Nannaethiops*, *Neolebias* (the *Neolebias*, *Congocharax* and *Dundocharax* of previous authors), *Paradistichodus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax* in the family (or subfamily). Reference to the proposed phylogeny shows, however, that such a classification results in the family representing a grade level assemblage. This gradal taxon forms a series of sister groups to a unit composed of *Hemistichodus*, *Ichthyborus* (the *Ichthyborus*, *Phagoborus* and *Gavialocharax* of previous authors), *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This latter assemblage constitutes the family Ichthyboridae or subfamily Ichthyborinae of earlier classifications. In light of the proposed phylogeny we can see that under previous classifications, some distichodontids would be more closely related to ichthyborids than to members of their own family. However, the retention of a gradistic, non-monophyletic taxon is untenable under the systematic procedures adopted as a basis for this study. Consequently, the family Ichthyboridae of Greenwood *et al.* (1966) (the Ichthyborinae of various authors) is sunk into the family Distichodontidae. The family Distichodontidae in this broader sense now forms a monophyletic group within characoids.

As discussed previously, the genera *Congocharax* and *Dundocharax* are placed as synonyms of *Neolebias* in order to resolve the previously non-monophyletic nature of *Neolebias*. The genera *Phagoborus* and *Gavialocharax*, in turn are synonymized into *Ichthyborus* as a consequence of the previous non-monophyly of *Phagoborus*. Finally, although the monophyly of *Distichodus*, *Nannocharax* and *Hemigrammocharax* is refuted or cast into doubt by the results of this study, these taxa are tentatively retained until such time as the subunit they form in the Distichodontidae can be studied in depth.

To summarize, the proposed classification of these families is as follows:

Family Citharinidae
    Genus *Citharinus* Cuvier, 1817
    Genus *Citharidium* Boulenger, 1902

Family Distichodontidae
  Genus *Xenocharax* Günther, 1867
  Genus *Nannaethiops* Günther, 1871
  Genus *Neolebias* Steindachner, 1894
  Genus *Paradistichodus* Pellegrin, 1922
  Genus *Distichodus* Müller and Troschel, 1845
  Genus *Nannocharax* Günther 1867
  Genus *Hemigrammocharax* Pellegrin, 1922
  Genus *Hemistichodus* Pellegrin, 1900
  Genus *Ichthyborus* Günther, 1864
  Genus *Microstomatichthyoborus* Nichols and Griscom, 1917
  Genus *Mesoborus* Pellegrin, 1900
  Genus *Eugnatichthys* Boulenger, 1898
  Genus *Paraphago* Boulenger, 1899
  Genus *Phago* Günther, 1865
  Genus *Belonophago* Giltay, 1929

The question of the relationship of the unit formed by citharinids and distichodontids to other characoids has not been resolved within this study. Various characters, such as the possession of a suprapreopercle, the lack of an interdigitating symphyseal dentary hinge and the anterior shift of the olfactory lobe, occur in groups outside of these families. However, in most cases these outgroups can be shown to be part of larger assemblages whose other members lack the apomorphous character in question. The characoid outgroup that has the greatest number of hypothesized apomorphous characters similar to those of, or occurring within, the unit formed by citharinids and distichodontids, is the Neotropical family Parodontidae. These bottom-dwelling fish, whose sister group is presently undetermined, have an anteriorly trifurcate supraethmoid articulating with the premaxillary articular fossae of the posteroventrally shifted upper jaw. Furthermore, parodontids have a slight anterior shift of the olfactory lobes and a distichodontid type of contact between the lateral ethmoid and orbitosphenoid. Such characters in isolation place parodontids close to the distichodontid genus *Nannocharax*. However, an overall analysis of parodontid anatomy reveals a series of inconsistencies with such an hypothesis. The Parodontidae lack a series of the synpapomorphies defining the unit formed by citharinids and distichodontids including: the modifications of the pars sustentaculum of the Weberian apparatus, the fusion of hypurals 1 and 2, the bicuspidate tooth form, the fusion of postcleithra 2 and 3, the separate suprapreopercle, the ovoid third posttemporal fossa bordered by the epioccipital and exoccipitals and the bifurcate pelvic bone. Furthermore, parodontids lack most of the numerous synapomorphies for distichodontids and for subunits of the Distichodontidae that include *Nannocharax*. Because of the absence of these characters in parodontids and because of other incongruities, it is impossible either to place the Parodontidae as part of a unit formed by the Citharinidae and Distichodontidae within characoids or to consider them as a sister group to that unit. A resolution of this problem posed by the seemingly independent acquisition of various apomorphous characters in parodontids and certain subunits of citharinids and distichodontids awaits a better understanding of characoid interrelationships.

Comparisons with previous classifications

As noted above, the classification arrived at in this study differs from those of Boulenger (1909) and Greenwood *et al.* (1966) which recognized two families or subfamilies within the group forming the family Distichodontidae of this study. Whereas such a division was the most commonly accepted classificatory scheme for the last three-quarters of a century, some workers divided citharinids and distichodontids along different lines. Regan (1911, pp. 21–23) recognized five subfamilies, one of which, his Xenocharacinae, was non-monophyletic according to the phylogeny proposed in this work. Eigenmann (1909, pp. 253–255) also recognized five subfamilies, but with different limits. Although he did not specifically list the genera assigned to each of the taxa, Eigenmann's key shows both his Neolebiinae and Ichthyborinae to be non-monophyletic, even allowing for the fewer species and genera described at that time. Subsequently, Gregory & Conrad (1938, p. 350) expanded the subfamily Citharininae to include *Citharinus*, *Citharidium*, *Nannaethiops*, *Neolebias*, *Xenocharax* and *Hemistichodus*. Their Distichodontinae, in turn, was composed of the genera *Distichodus*, *Nannocharax*, *Ichthyborus*, *Mesoborus*, *Phagoborus*, *Eugnatichthys*, *Paraphago* and *Phago*. However, a comparison of the limits of these taxa with the phylogeny here proposed shows that neither of Gregory & Conrad's subfamilies represents a monophyletic unit. That is, neither contains all the descendants of its hypothesized common ancestor. Monod (1950, p. 58) recognized three subfamilies, Citharininae, Distichodontinae and Ichthyborinae, within the group under discussion. However, his definition of the Distichodontinae (characterized by the 'Articulaire et dentaire articulés par chevauchement latéral . . .' – the *Distichodus* form of lower jaw) excludes *Neolebias*, *Nannaethiops*, *Xenocharax* and *Paradistichodus* from that subfamily. Furthermore, these genera are similarly excluded from the Citharininae and Ichthyborinae under Monod's definition of those subfamilies. Finally, Poll (1973, Fig. 1) lists his Citharininae as consisting of *Citharinus*, *Citharidium*, *Xenocharax*, *Nannaethiops*, *Neolebias*, *Dundocharax*, *Paradistichodus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax* (on p. 114 of his paper he stated that there are eleven citharinid genera. The missing genus of his Fig. 1 appears to be *Congocharax*). The expansion of the family Citharinidae by this group of nominal distichodontid genera, although resolving the non-monophyly of the Distichodontidae (sensu Greenwood *et al*., 1966), as a consequence of the elimination of the taxon, simultaneously converts the previously monophyletic Citharinidae into a gradal non-monophyletic group.

Comments on the African Characidae

In the course of outgroup comparisons involved in this study of the Citharinidae and Distichodontidae, several characters of relevance to an understanding of the hypothesis of the monophyly of the African Characidae and to relationships within African characids were found. As noted by Roberts (1969, p. 441) the shape of the upper jaw and dentition is distinctive for African characids among characoids. Furthermore, all African characids examined during this study, with the exception of *Lepidarchus*, have a small third posttemporal fossa totally contained within the epioccipital. The possession of this apomorphous character together with the unique jaw and dental modifications described above is consistent with the hypothesis that the African Characidae forms a monophyletic subunit of characoids.

Thus on the basis of available information, African characoids can be assigned to three monophyletic groups: the unit formed by the Citharinidae and Distichodontidae; the assemblage formed by the members of the African Characidae; and the monotypic family Hepsetidae. However, relationships of these groups to each other and to Neotropical characoids are presently undetermined.

Several other characters are of relevance for an understanding of the relationships within the African Characidae and for questions on the validity of the presently recognized generic and suprageneric taxa in this group. In the course of the discussion on the morphology of the anterior orbital region, it was noted that a bony tube surrounding the olfactory tract and bulb was described by Starks (1926, p. 167) for *Alestes liebrechstii* and *A. grandisquamis*. More recently Roberts (1969, p. 441) also noted this orbitosphenoid process in *Alestes baremose*, *A. imberi*, *A. marcolepidotus*, *Bryconaethiops* and *Hydrocynus*, and it has also been found in *Alestes dentex* and *A. macrophthalmus* during this study. This bony tube, which is lacking in all other African characids examined, is hypothesized as being apomorphous for these taxa among characoids on the basis of ontogenetic and outgroup comparisons. Those species with an orbitosphenoid tube also have the premaxillae joined by interpremaxillary interdigitations. As discussed earlier, both the broadened contact of the premaxillae anterior to the supraethmoid spine, and the associated symphyseal interdigitations are considered apomorphous and thus indicative of the monophyletic nature of the assemblage formed by the taxa possessing them. Congruent with these apomorphic modifications of the premaxillae and orbitosphenoid is the forward shift of the olfactory bulb in *Hydrocynus*, *Bryconaethiops* and various *Alestes* species (*imberi*, *dentex*, *liebrechstii*, *macrophthalmus*, *macrolepidotus*, *nurse*, *rhodopleura* and *lateralis;* the condition of the orbitosphenoid and premaxillae is unknown for the last three species). Such a derived anterior shift of the olfactory bulb is lacking among the other *Alestes* species and African characid genera examined. On the basis of these characters (the orbitosphenoid tube, the anterior shift of the olfactory bulb and the interdigitation of the premaxillae) it appears that the above *Alestes* species and the genera *Bryconaethiops* and *Hydrocynus* form a monophyletic subunit of the African Characidae.

Further studies are required to determine the exact distribution of the above derived osteology and neurological characters within African characids. Nonetheless, the available evidence contraindicates the inherent hypotheses of the monophyly of the genus *Alestes* and the subfamily Alestiinae as now defined. The genus *Alestes*, in its present sense, does not form a monophyletic unit in so far as the distribution of apomorphous characters indicates that some of its members are more closely related to species of the genera *Bryconaethiops* and *Hydrocynus* than to the remaining *Alestes* species. A redefinition of *Alestes* as a monophyletic unit must, however, await a detailed anatomical study of African characids and a phylogenetic analysis based on information from derived characters, both those discussed previously and others.

Roberts (1969, p. 442) divided the African Characidae into two subfamilies. These were the Hydrocyninae limited to the genus *Hydrocynus* and the Alestiinae for all other African characids. However, although the Hydrocyninae of such a classificatory scheme represents a monophyletic unit, the Alestiinae of that system is an unnatural grouping. As detailed above, the genera *Hydrocynus* and *Bryconaethiops* share a series of derived characters and form a monophyletic assemblage with some *Alestes* species. Consequently, a subdivision of African characids into two subfamilies along the lines proposed by Roberts results in some members of the subfamily Alestiinae (*Bryconaethiops* and various *Alestes* species) being more closely related to members of another subfamily (Hydrocyninae) than they are to the remaining taxa within their own subfamily. Thus the Alestiinae of Roberts must be considered a gradal non-monophyletic assemblage. Although the exact distribution of the derived characters discussed above is undetermined, the evidence is sufficient to indicate that the Hydrocyninae of Roberts (1969) should be sunk into the Alestiinae in order to resolve the present non-monophyly of the latter subfamily. The Alestiinae in this broader sense forms an evidently monophyletic assemblage within the Characoidea.

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